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COMPARATIVE HISTOLOGY OF RADULA-SUPPORTING STRUCTURES IN GASTROPODA

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ABSTRACT

A comparative histological study was undertaken to reveal the morphological diversity and systematic characters of a radula-supporting organ of gastropods. Observations on 33 species, all from different families, revealed six major morphological characters: (1) the number of odontophoral cartilages or radular bolsters: 0, 1 (fused), 2, 4, 5, 6 and 10; (2) histology categorized into 6 types based on the properties of cartilage matrix and cells; (3) the presence or absence of an enclosing membrane of the cartilages or radular bolsters; (4) the presence or absence of overlapping of the right and left cartilages or radular bolsters; (5) the closest position of the cartilages or radular bolsters to each other in cross section at ventral or dorsal side; and (6) the insertion areas of the ventral approximator muscle connecting the cartilages or radular bolsters – ventral, medial, or outer lateral area. Outgroup and ingroup comparisons based on recent phylogenetic hypotheses suggest the following evolutionary scenario for gastropod radula-supporting organs: the ancestral gastropod is assumed to have possessed two pairs of odontophoral cartilages with a thick matrix and ventrally connected by the approximator muscle. The cartilages have possibly independently increased in number in patellogastropods and Neritimorpha, decreased into a one pair, single piece or lost in Caenogastropoda, and replaced by connective tissue and muscle fibers in Heterobranchia. Some taxa such as Cypraeidae have gained a unique histology. The cartilages or radular bolsters are closest ventrally in cross section in the majority of gastropods but closest dorsally in part of the taenioglossate Caenogastropoda. The diversification of these character states in gastropods seems to be phylogenetically constrained, not ecologically.

Key words: odontophore, odontophoral cartilage, radular bolster, ventral approximator muscle, histology, morphological diversity, Gastropoda.

INTRODUCTION

Gastropoda has gained the most diversified anatomy and ecology among the nine classes of the phylum Mollusca and are therefore an interesting subject for comparative anatomy (e.g., Haszprunar, 1988a; Ponder & Lindberg, 1997). In phylogenetic studies, morphology-based cladistic analyses have been carried out using more than 100 anatomical characters for gastropods (Salvini-Plawen & Steiner, 1996; Ponder & Lindberg; 1997; Sasaki, 1998; Barker, 2001; Dayrat & Tillier, 2002; Strong, 2003). Among them, feeding structures (radular, odontophore and related structure) provide a number of characters useful for higher phylogeny and are of great importance in comparative morphology.

Concerning radula-supporting structure, the presence or absence of the cartilages and the number of cartilage pairs have been verified to define higher taxonomic groups of gastropods (Salvini-Plawen & Steiner, 1996: character #22 for Strepeneura; Ponder & Lindberg; 1997: #68; Sasaki, 1998: #54–56; Barker, 2001: #2; Dayrat & Tillier, 2002: #34; Strong, 2003: #13). Most notably, cartilage-less Heterobranchia is contracted by cartilage-bearing "prosobranchs" (see above for references). The revision of published data, however, suggests greater diversity potentially exists in cartilage morphology and histology, but they have not been fully investigated across major gastropod groups comparatively (see Discussion for source of previous descriptions). In addition, there has been some confusion in the

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use of terms (odontophore, cartilages, bolsters, etc.) and interpretations of homology among different molluscan classes.

In a search for useful systematic characters in gastropods, we attempted a comparative study of radula-supporting organs. Based on new results, we categorize discrete character states of various parts, summarize their taxonomic distribution in gastropods, and discuss their systematic implications, homology, and relevance to ecology.

MATERIAL AND METHODS

Living specimens of 33 species belonging to 33 families of Gastropoda were collected from various environments covering terrestrial, fresh- and blackish-water, intertidal to bathyal environments in Japan (Table 1). After removal from the shell, the soft parts of animals were fixed in 4% formalin, preserved in 70% ethanol, and dissected under a binocular microscope. For histological sectioning, a head containing the buccal mass was dehydrated with a series of ethanol, embedded in paraffin, serially cross-sectioned at the thickness of 4, 6 or 8 µm, and stained by Heidenhain's Azan method in which collagenous tissues are stained in blue and muscle fibers are in red. Histology of radular-supporting organs was observed under a light microscope and photographed. Systematics at family or higher level in this paper follows Bouchet & Rocroi (2005).

Abbreviations

ac	anterior cartilage
alc	anterolateral cartilage
cc	cartilage cell
ct	connective tissue
e	extramatrix substance
es	esophagus
fc	fibrous connective tissue
ic	inner cartilage
m	cartilage matrix
mc	median cartilage
mf	muscle fiber
n	nucleus
oc	odontophoral cartilage
ouc	outer cartilage
pc	posterior cartilage
pdc	posterodorsal cartilage
ra	radula
rb	radular bolster
rv	radular vesicle
te	tendon-like structure
va	ventral approximator muscle
vad	ventral approximator muscle dorsal layer
vav	ventral approximator muscle ventral layer
vc	ventral cartilage

Terminology

Revision and redefinition of the descriptive terms for molluscan radular-supporting organs are necessary because different terminology has been used for similar structures by various authors in the past. We redefine these terms below.

The *cartilage* or *odontophoral cartilage* are widely used terms (e.g., Fretter & Graham, 1962: 177; Hubendick, 1978: 13; Salvini-Plawen, 1988: 331; Ponder & Lindberg, 1997: 145; Sasaki, 1998; Sasaki et al., 2006a, b), but has been used without definition in most cases. In this study, we define the odontophoral cartilages in gastropods as follows: rigid structure(s) in the odontophore composed exclusively of similar-sized turgescent cells partitioned by an extracellular matrix. This definition is consistent with a general and broad definition of invertebrate cartilages based on the presence of an extracellular matrix (Cole & Hall, 2004).

The *bolster* or *radular bolster* is another widely used term (Hyman, 1967: 241; Salvini-Plawen, 1988: 329; Scheltema et al., 1994: 40; Voltzow, 1994: 167; Shimek & Steiner, 1997). It has not been defined histologically but used for any massive structure supporting the radula within the odontophore. However, to emphasize histological differences from the odontophoral cartilages defined above, we use this term for any radula-supporting structures that possess the identical topology with odontophoral cartilages, but lacking true cartilaginous tissue, as in Heterobranchia.

The *odontophore* is sometimes used for a supporting structure lacking the cartilage (e.g., Mackenstedt & Märkel, 2001) or synonymous with the radular bolster (Voltzow, 1994: 167). However, the term is also equivalent to the term *buccal mass* in some literature (e.g., Fretter & Graham, 1962: 153). To avoid confusion, we apply the term odontophore to a larger unit containing the radula, radula-supporting structures (odontophoral cartilages and/or radular bolsters) and their connecting muscles, as has been widely used (e.g., Hyman, 1967; Hubendick, 1978: 13; Salvini-Plawen, 1988: 329; Sasaki, 1998).

The *radular vesicle* has been applied exclusively to hollow fluid-filled radula-supporting structures found in Polyplacophora (Wingstrand, 1985) and Monoplacophora (Lemche & Wingstrand, 1959; Wingstrand, 1985; Schaefer & Haszprunar, 1996; Haszprunar & Schaefer, 1996, 1997). Based on clear differences in its inner structure from other similar odontophoral cartilages, the use of this term should be restricted to those two classes.

TABLE 1. Sampling data of material examined in this study. All localities are in Japan.

Higher Taxa	Species	Locality and Sampling Date
Polyoplacophora		
Ischnochitonidae	*Ischnochiton comptus*	Misaki, Miura Peninsula, June 3–5, 2004
Scaphopoda		
Dentaliidae	*Dentalium octanglatum*	Koajiro Bay, Miura Peninsula, Nov. 12, 2001
Gadilinidae	*Episiphon subrectum*	Off Katsuura, Wakayama Prefecture, 51–59 m, R/V *Tansei-maru*, cruise KT-99-17, station KU4, Nov. 29, 1999
Patellogastropoda		
Nacellidae	*Cellana grata*	Takeoka, Futtsu, Chiba Prefecture, May 25, 2002
Vetigastropoda		
Haliotidae	*Haliotis diversicolor aquatilis*	Fish market in Tokyo, Aug. 1, 2003
Trochidae	*Monodonta labio* forma *confusa*	Jogashima Island, Misaki, Kanagawa Prefecture, June 5, 2004
Cocculiniformia		
Cocculinidae	*Cocculina* sp. cf. *japonica*	Off Hino-Misaki, Shimane Prefecture, 397–404 m, R/V *Tansei-maru*, cruise KT-98-17, station 8, Sep. 27–28, 1998
Neritimorpha		
Neritidae	*Nerita albicilla*	Jogashima Island, Misaki, Kanagawa Prefecture, June 5, 2004
Taenioglossate Caenogastropoda		
Cyclophoridae	*Cyclophorus herklotsi*	Minakawa, Kuroshio, Kouchi Prefecture, April 24, 1999
Viviparidae	*Cipangopaludina chinensis laeta*	Ikura, Wakasa, Fukui Prefecture, June 20, 2002
Batillariidae	*Batillaria cumingii*	Aburatsubo, Misaki, Kanagawa Prefecture, June 5, 2004
Calyptraeidae	*Crepidula onyx*	Kisarazu, Chiba Prefecture, June 2003
Cypraeidae	*Cypraea boivinii*	Aburatsubo, Misaki, Kanagawa Prefecture, Aug. 3, 2003; Banda, Tateyama, Chiba Prefecture, Sep. 27–28, 1998
Littorinidae	*Littorina brevicula*	Jogashima Island, Misaki, Kanagawa Prefecture, April 24, 2004; Odaiba, Tokyo, April 28, 2004
Naticidae	*Glossaulax didyma*	Kisarazu, Chiba Prefecture, June, 2003
Assimineidae	*Assiminea japonica*	Mihama, Fukui Prefecture, June 20, 2002
Strombidae	*Strombus luhuanus*	Uehara, Iriomote Island, Okinawa, May 10, 2004
Ranellidae	*Fusitriton oregonensis*	Otsuchi, Iwate Prefecture, July 15, 1999
Hipponicidae	*Hipponix conica*	Fish market in Tokyo, Aug. 20, 2003
Vermetidae	*Serpulorbis imbricatus*	Jogashima Island, Misaki, Kanagawa Prefecture, May 20, 2003

(continues)

(continued)

Higher Taxa	Species	Locality and Sampling Date
Neogastropoda		
Buccinidae	*Japeuthria ferrea*	Jogashima Island, Misaki, Kanagawa Prefecture, April 24, 2004
Columbellidae	*Euplica scripta*	Jogashima Island, Misaki, Kanagawa Prefecture, June, 2003
Nassariidae	*Nassarius festiva*	Kisarazu, Chiba Prefecture, June, 2003
Muricidae	*Thais clavigera*	Jogashima Island, Misaki, Kanagawa Prefecture, April 24, 2004
Mitridae	*Strigatella zebra*	Hoshizunano-hama, Iriomote Island, Okinawa, May 13, 2004
Conidae	*Conus ebraeus*	Hoshizunano-hama, Iriomote Island, Okinawa, May 13, 2004
Heterobranchia		
Haminoeidae	*Haloa japonica*	Jogashima Island, Misaki, Kanagawa Prefecture, May 20, 2003
Philinidae	*Philine argentata*	Lake Hamana, Shizuoka Prefecture, Aug. 1996
Cylichnidae	*Nipponoscaphander japonica*	Off Katsuura, Wakayama Prefecture, 99–102 m, R/V *Tansei-maru*, cruise KT-99-17, station KU5, Nov. 30, 1999
Cavoliniidae	*Cavolinia uncinata*	Off Izu Islands, R/V *Shinyo-maru* sta. 1998-L1, Oct. 19, 1998
Aplysiidae	*Aplysia oculifera*	Jogashima Island, Misaki, Kanagawa Prefecture, May 20, 2003
Chromodorididae	*Hypselodoris festiva*	Arasaki, Yokosuka, Kanagawa Prefecture, June 23, 2002; Jogashima Island, Misaki, Kanagawa Prefecture; Aug. 14, 2003; Aburatsubo, Misaki, Kanagawa Prefecture; June 3–5, 2004
Siphonariidae	*Siphonaria japonica*	Jogashima Island, Misaki, Kanagawa Prefecture, April 24, 2004; Jogashima Island, Misaki, Kanagawa Prefecture, Aug. 1, 2003
Lymnaeidae	*Lymnaea stagnalis*	Aqualium in The University of Tokyo, 2003
Onchidiidae	*Peronia* sp. cf. *verruculatum*	Aburatsubo, Misaki, Kanagawa Prefecture, Aug. 1, 2003
Bradybaenidae	*Acusta despecta sieboldiana*	Omachi, Nagano Prefecture, July 2002

RESULTS

Clade Patellogastropoda
Superfamily Nacelloidea
Family Nacellidae

Cellana grata (Gould, 1859)
(Figs. 1A, 2)

Odontophore containing five pairs of cartilages – anterior (ac), anterolateral (alc), ventral (vc), posterodorsal (pdc), posterior cartilages (pc) (Figs. 1A, 2A–C). Anterior and anterolateral cartilages larger than posterior ones (Fig. 1A), former especially elongate. Anterolateral cartilages attached to anterolateral side of anterior cartilages, ventral cartilages to anteroventral side. Posterior cartilages overlying posterior end of anterior cartilages; posterodorsal cartilages closely anterior to posterior cartilages. All cartilages except anterior one show similar histology having stiffened matrix (m) and cartilage cells (cc) containing small nuclei (n) that tend to be

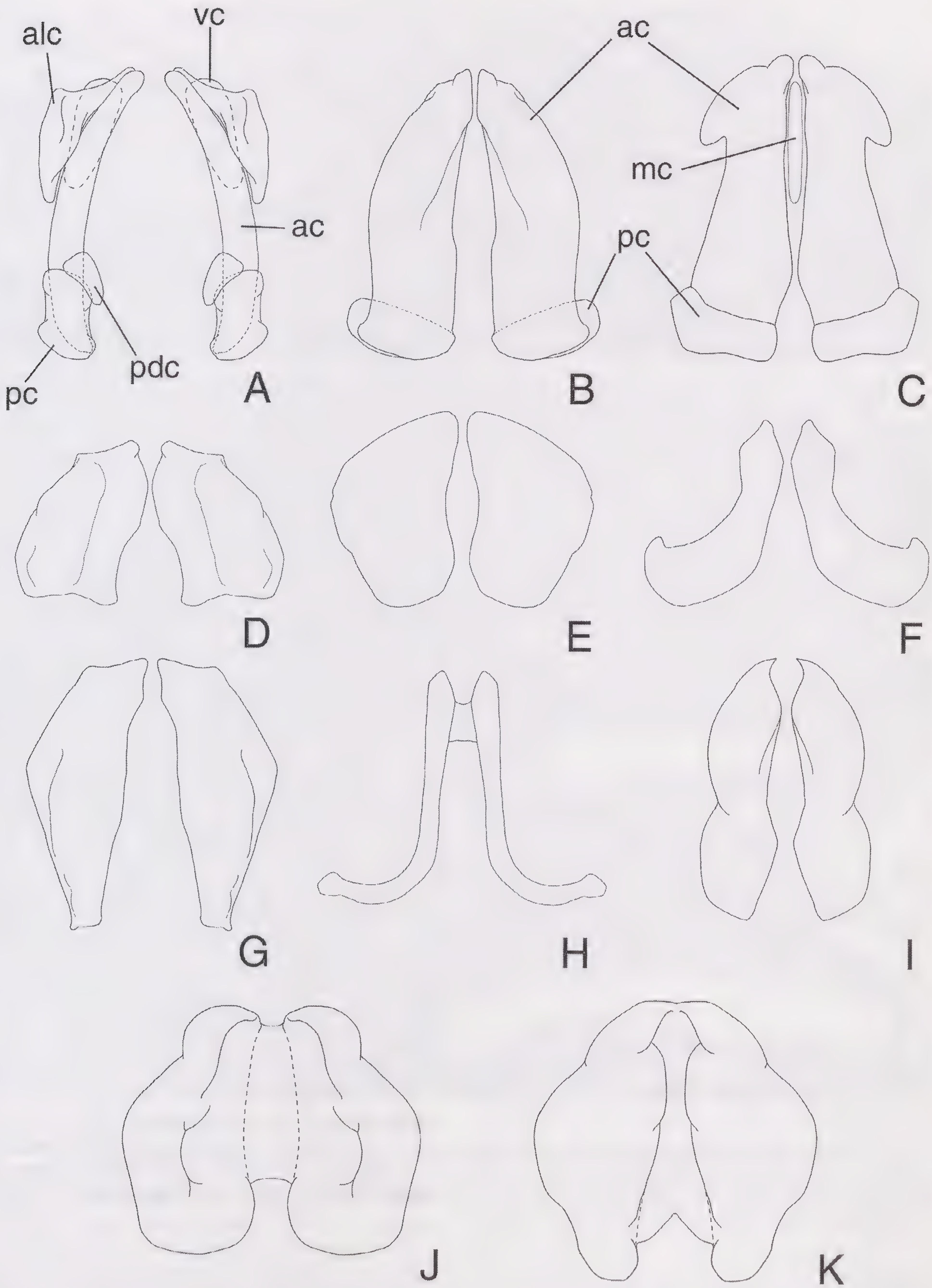

FIG. 1. Outline of odontophoral cartilages. A: *Cellana grata* (Nacellidae); B: *Haliotis diversicolor aquatilis* (Haliotidae); C: *Nerita albicilla* (Neritidae); D: *Cipangopaludina chinensis laeta* (Cyclophoridae); E: *Littorina brevicula* (Littorinidae); F: *Crepidula onyx* (Calyptraeidae); G: *Cypraea boivinii* (Cypraeidae); H: *Thais clavigera* (Muricidae); I: *Strigatella zebra* (Mitridae); J: *Peronia* sp. cf. *verruculatum* (Onchidiidae); K: *Acusta despecta sieboldiana* (Bradybaenidae). All dorsal views.

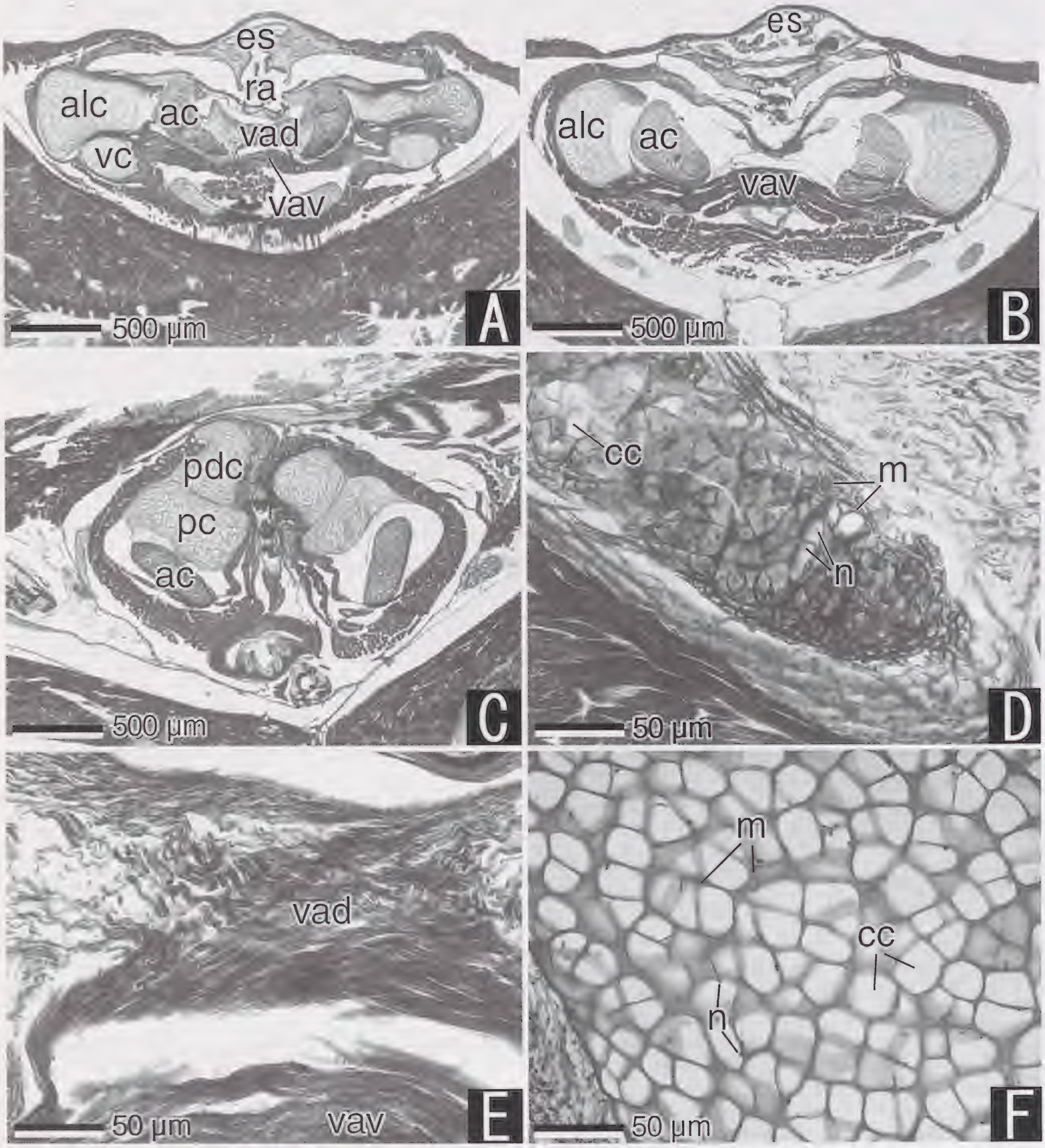

FIG. 2. Cross sections of buccal mass and odontophoral cartilages of *Cellana grata* (Nacellidae). A: Anterior part of buccal mass; B: Middle part of buccal mass; C: Posterior part of buccal mass; D: Enlarged view of anterior cartilage; E: Dorsal and ventral layers of ventral approximator muscle; F: Enlarged view of anterolateral cartilage.

located close to matrix (Fig. 2F). Cells of anterior cartilages smaller and denser than those of other cartilages (Fig. 2D). Anterior cartilages not fused or overlapped, closest to each other ventrally in cross section (Fig. 2A–C), connected by two-layered ventral approximator muscle (Fig. 2A, E); dorsal layer (vad) inserting at anteromedian area of anterior cartilages (Fig. 2A); ventral layer (vav) connecting ventral plane of anterior cartilages (Fig. 2A, B).

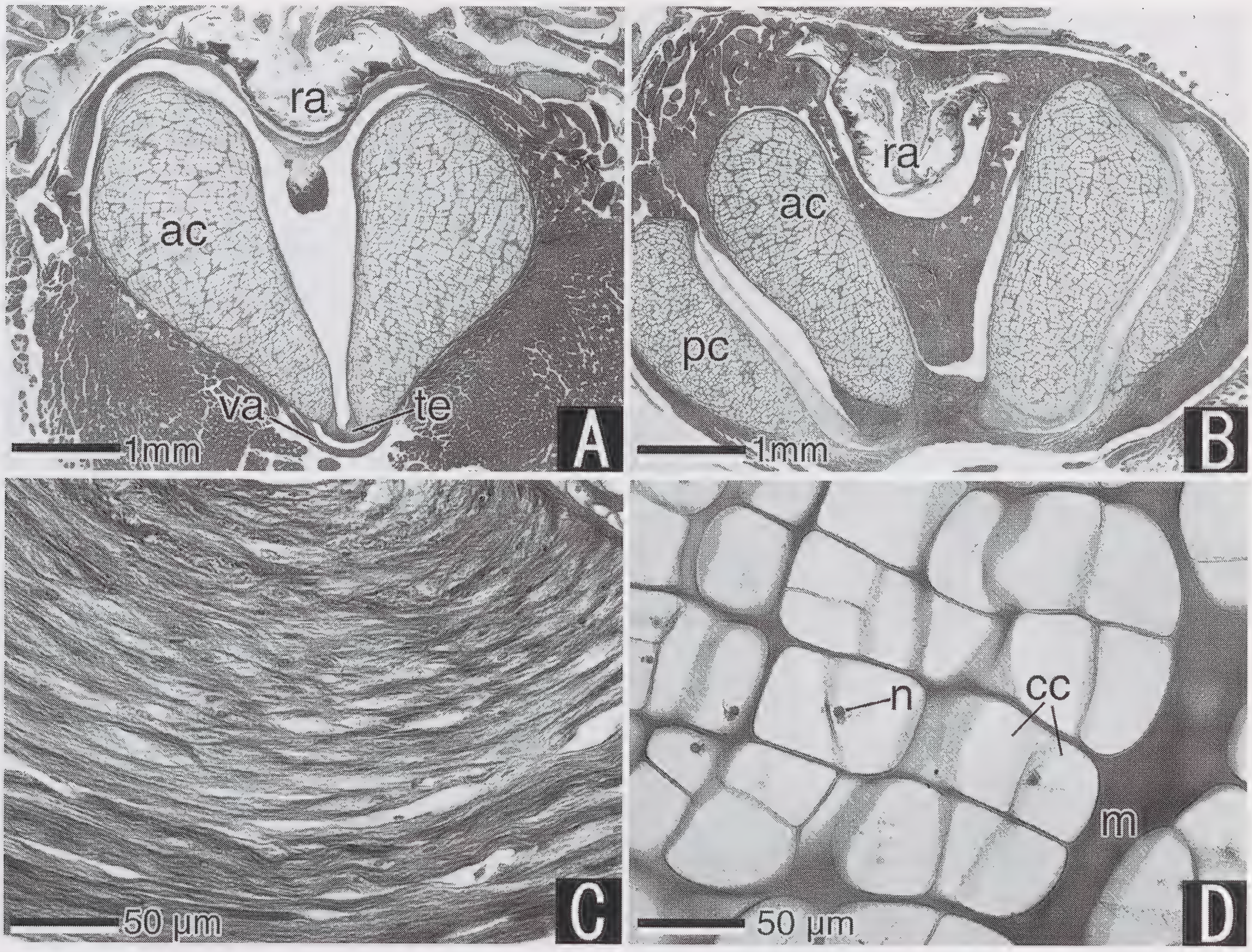

FIG. 3. Cross sections of buccal mass and odontophoral cartilages of *Haliotis diversicolor aquatilis* (Haliotidae). A: Middle part of buccal mass; B: Posterior part of buccal mass; C: Enlarged view of ventral approximator muscle; D: Enlarged view of anterior cartilage.

Clade Vetigastropoda
Superfamily Haliotoidea
Family Haliotidae

Haliotis diversicolor aquatilis Reeve, 1846
(Figs. 1B, 3)

Odontophore containing two pairs of cartilages – anterior and posterior cartilages (ac, pc: Fig. 3A, B). Posterior cartilages smaller than anterior cartilages, adhering to posterior end of anterior cartilages (Fig. 1B: see Sasaki, 1998: fig. 31, for gross morphology). Both cartilages consisting of robust matrix (m), cartilage cells (cc) containing small nuclei (n) frequently attached tightly to matrix (Fig. 3D). Anterior cartilages not fused or overlapped, facing each other most closely ventrally in cross section, connected with tendon-like structure (te) (Fig. 3A) and thin layer of ventral approximator muscle (va) (Fig. 3A, C).

Superfamily Trochoidea
Family Trochidae

Monodonta labio confusa Tapparone-Canefri, 1874
(Fig. 4)

Odontophore containing two pairs of cartilages, *viz.* anterior and posterior cartilages (ac, pc: Fig. 4A, B). Both cartilages composed of stout matrix (m), cartilage cells (cc), with small nuclei (n) located close to matrix (Fig. 4D). Posterodorsal parts of anterior cartilages containing characteristic dense zone of thin matrix and cells (asterisk in Fig. 4A; magnified in Fig. 4C). Anterior cartilages not fused or overlapped, closest ventrally in cross section, connected by ventral approximator muscle (va) including fibrous connective tissue (Fig. 4A). Ventral approximator muscle inserting at ventral side of anterior cartilages (Fig. 4A).

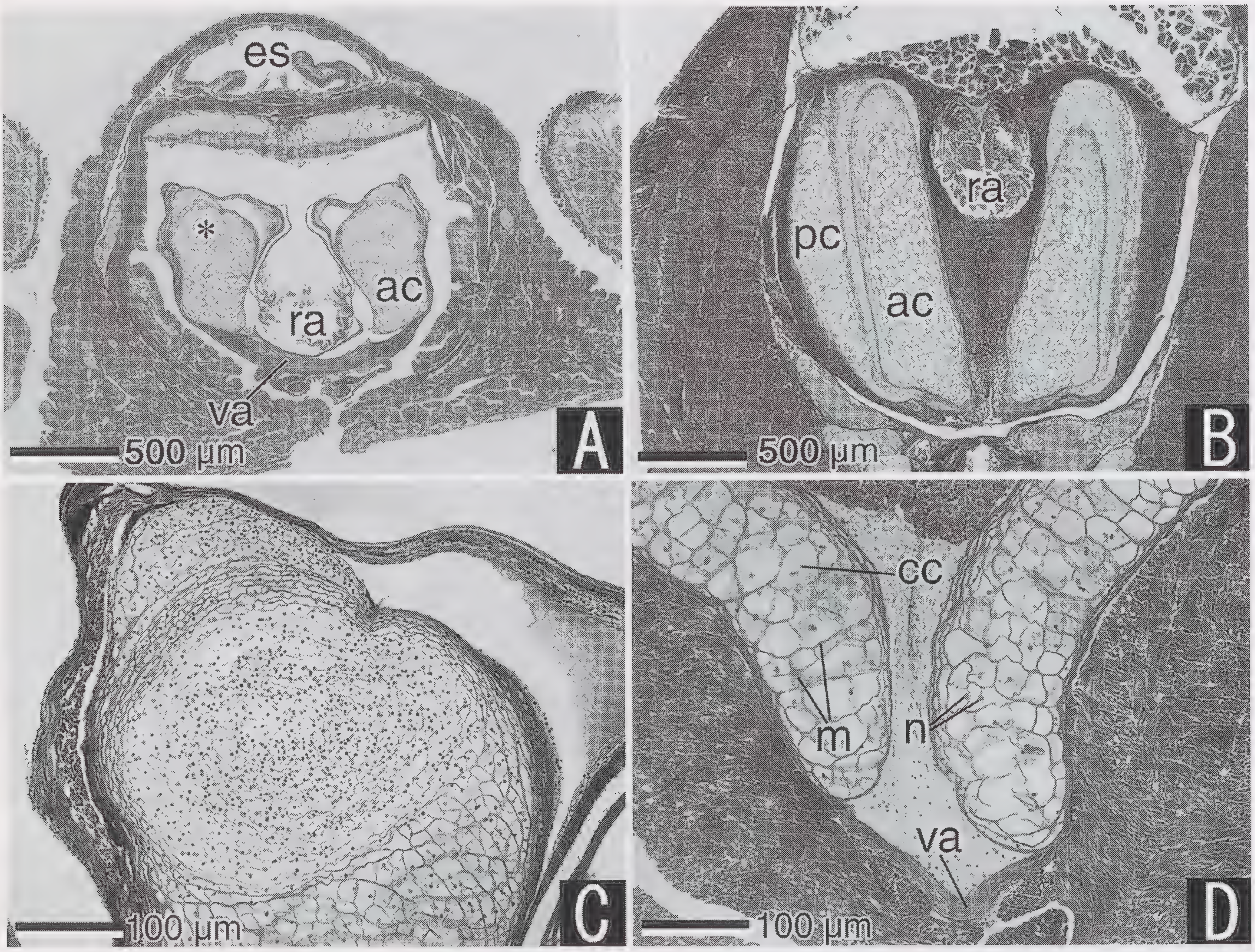

FIG. 4. Cross sections of buccal mass and odontophoral cartilages of *Monodonta labio confusa* (Trochidae). A: Anterior part of buccal mass. Asterisk indicates a mass of smaller cells; B: Posterior part of buccal mass; C: Enlarged view of part of anterior cartilage marked by asterisk in Fig. A; D: Enlarged view of anterior cartilage.

Clade Cocculiniformia
Superfamily Cocculinoidea
Family Cocculinidae

Cocculina sp. cf. *japonica* Dall, 1907
(Fig. 5A, B)

Odontophore containing single pair of cartilages (oc: Fig. 5A) consisting of cartilage cells (cc) and matrix (m). Cartilage matrix consisting of two elements: (1) thick sheets of matrix at nearly constant spacing that divide cartilages into multiple horizontal sectors of nearly equal size; (2) extremely thin matrix connecting horizontal sheets obliquely or vertically (Fig. 5B). Nuclei (n) of cartilage cells relatively large, mostly attached to matrix (Fig. 5B). Cartilages not fused along entire length, closest to each other ventrally without overlapping, and connected by connective tissue (ct) and by ventral approximator muscle (va) inserting at ventral side of cartilages (Fig. 5B).

Clade Neritimorpha
Superfamily Neritoidea
Family Neritidae

Nerita albicilla Linnaeus, 1758
(Figs. 1C, 5C–F)

Odontophore containing two pairs of cartilages (Fig. 1C) and single unpaired cartilage (Fig. 5C, F). Anterior and posterior cartilages composed of thick cartilage matrix (m), cartilage cells (cc), very small nuclei (n) beside matrix (Fig. 5D). Median cartilage showing similar histology but its matrix thinner than that of other cartilages (Fig. 5D). Anterior cartilages (ac) longitudinally elongate; posterior cartilages (pc) much smaller, attached to posterior end of anterior cartilages; median cartilage (mc) thin, club-shaped, inserted between anterior cartilages (Fig. 1C). Anterior cartilages unfused, closest ventrally without overlapping in cross section, connected at ventral level by

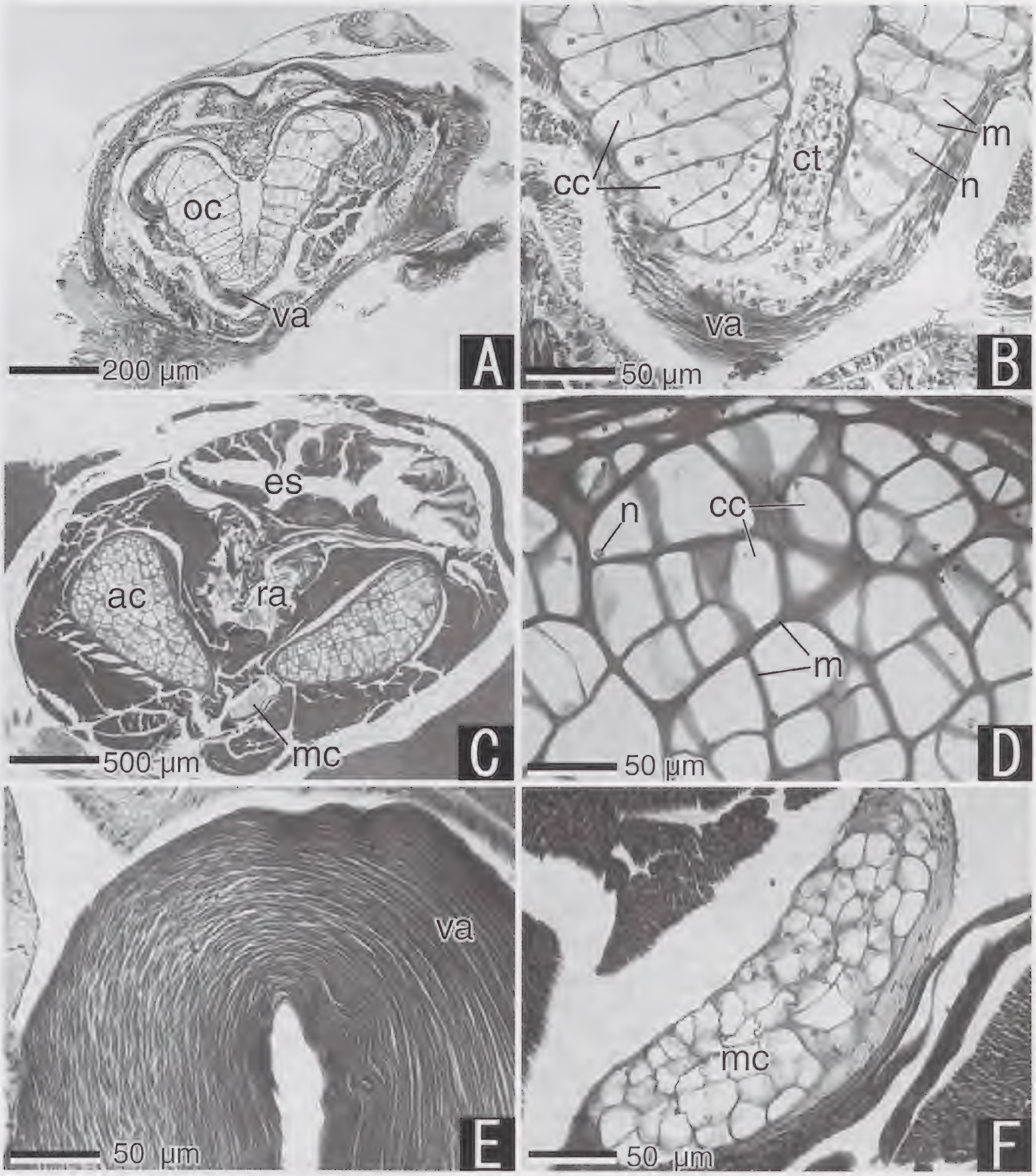

FIG. 5. Cross sections of buccal mass and odontophoral cartilages. A, B. *Cocculina* sp. cf. *japonica* (Cocculinidae). A: Section in middle part of buccal mass; B: Enlarged view of Fig. 5A to show histology of cartilages, ventral approximator muscle (va) and connective tissue (ct); C, F. *Nerita albicilla* (Neritidae). C: Section in middle part of buccal mass; D: Enlarged view of anterior cartilage; E: Enlarged view of ventral approximator muscle; F: Median cartilage.

ventral approximator muscle (va) inserting at ventral side (Fig. 5C).

Sasaki (1998: p. 111, fig. 75) described the median cartilage as a pair of symmetrical elements. However, the median cartilage is actually a single body in histological observations.

Clade Caenogastropoda
Informal group Architaenioglossa
Superfamily Cyclophoroidea
Family Cyclophoridae

Cyclophorus herklotsi Martens, 1861
(Fig. 6A, B)

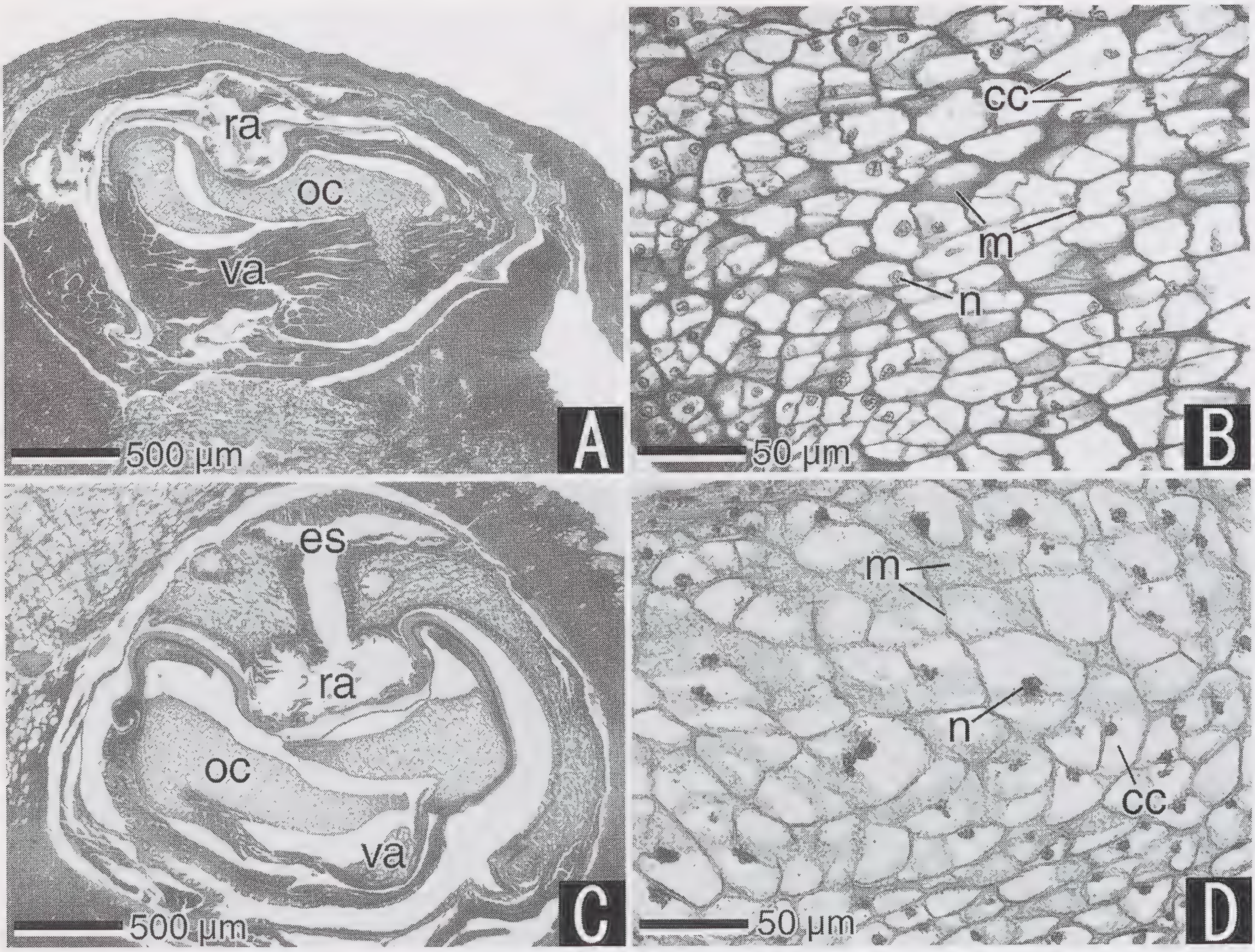

FIG. 6. Cross sections of buccal mass and odontophoral cartilages. A, B. *Cyclophorus herklotsi* (Cyclophoridae). A: Section in anterior part of buccal mass; B: Enlarged view of odontophoral cartilage; C, D. *Cipangopaludina chinensis laeta* (Viviparidae). C: Section in middle part of buccal mass; D: Enlarged view of odontophoral cartilage.

Odontophore containing single pair of unfused cartilages (oc) (Figs. 1D, 6A) with thin matrix (m), cartilage cells (cc), and nuclei (n) that are large in size relative to cartilage cells, located in various parts within them (Fig. 6B). Cartilages closest ventrally, connected by ventral approximator muscle (va) inserting at outer lateral side (Fig. 6A). Left cartilage partially overlying right cartilages.

Superfamily Viviparoidea
Family Viviparidae

Cipangopaludina chinensis laeta (Martens, 1860)
(Figs. 1D, 6C, D)

Odontophore containing single pair of unfused cartilages (oc: Fig. 6C) with thin matrix (m), cartilage cells (cc), relatively large nuclei (n) mostly in contact with matrix (Fig. 6B). Cartilages closest and connected ventrally by single-layered ventral approximator muscle (va) inserting at outer lateral side (Fig. 6C). Left cartilage underlying right cartilage.

Clade Sorbeoconcha
Superfamily Cerithioidea
Family Batillariidae

Batillaria cumingii (Crosse, 1862)
(Fig. 7A, B)

Odontophore containing single pair of unfused cartilages (oc) consisting of thin matrix (m), cartilage cells (cc) with relatively large nuclei (n) scattered in various areas inside of cells (Fig. 7B). Pair of cartilages overlapping ventrally, connected by ventral approximator muscle (va) inserting at outer lateral side of cartilages (Fig. 7A).

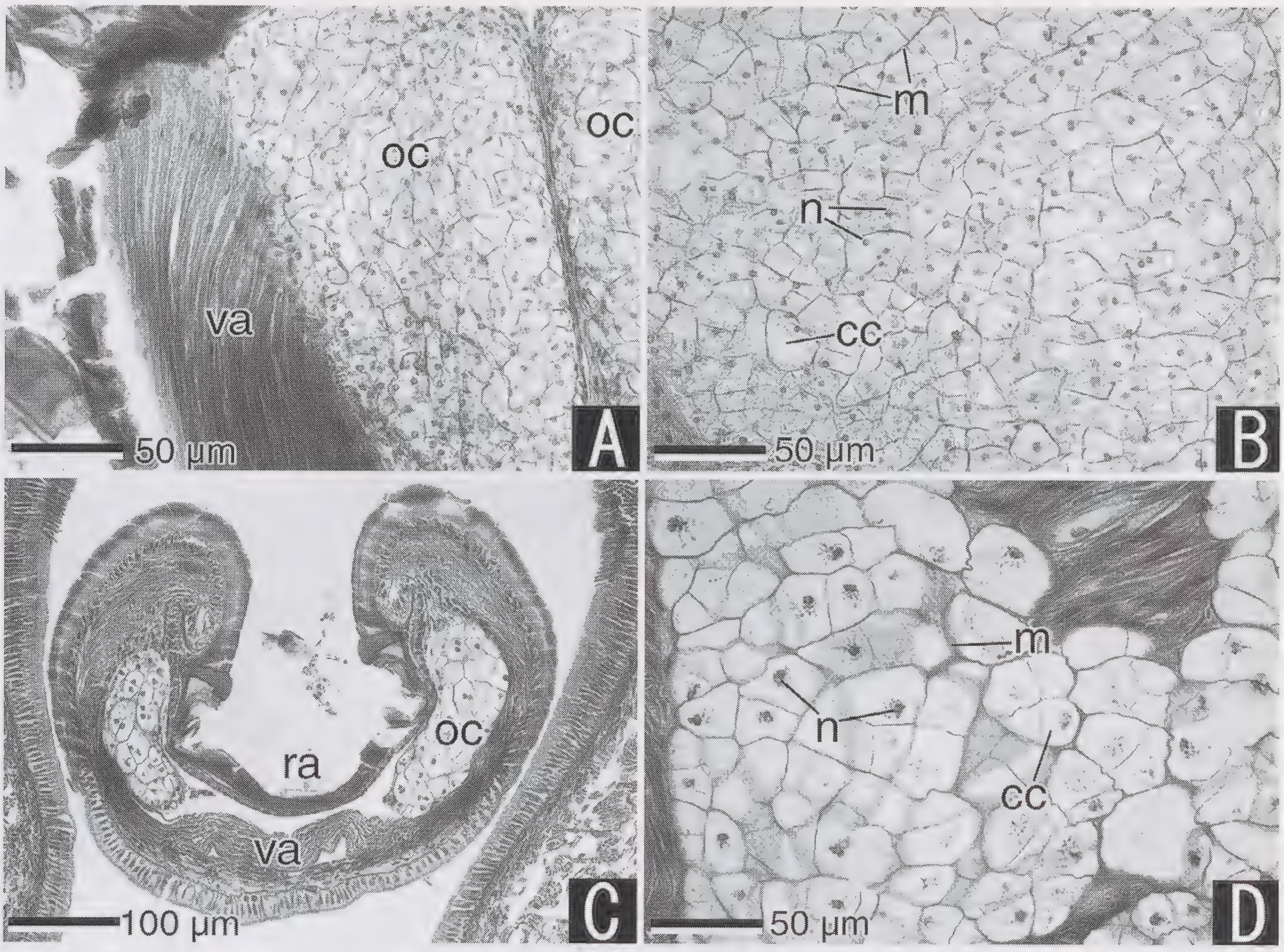

FIG. 7. Cross sections of buccal mass and odontophoral cartilages. A, B. *Batillaria cumingii* (Batillariidae). A: Outer lateral origin of ventral approximator muscle; B: Enlarged view of central part of odontophoral cartilage; C, D. *Crepidula onyx* (Calyptraeidae). C: Anterior part of buccal mass; D: Enlarged view of odontophoral cartilage.

Clade Hypsogastropoda
Clade Littorinimorpha
Superfamily Calyptoraeoidea
Family Calyptraeidae

Crepidula onyx G. B. Sowerby I, 1824
(Figs. 1F, 7C, D)

Odontophore containing single unfused pair of cartilages (oc: Figs. 1F, 7C) with thin matrix (m), cartilage cells (cc) and relatively large nuclei (n) located in various areas within cartilage cells (Fig. 7D). Cartilages closest ventrally without overlapping, connected by ventral approximator muscle (va) inserting at outer side of cartilages (Fig. 7C).

Superfamily Cypraeoidea
Family Cypraeidae

Cypraea boivinii Kiener, 1843
(Figs. 1G, 8)

Odontophore containing single unfused pair of cartilages (oc: Figs. 1G, 8A, B) consisting of markedly thick bubble-shaped matrix (m), with extramatrix substance (e) filling spaces between cartilage matrices, cartilage cells (cc) with small nuclei (n) located at various areas inside of cells (Fig. 8D). Matrix and extramatrix substance stained in blue and in red, respectively. Cartilages closest ventrally without overlapping and connected by ventral approximator muscle (va) inserting at ventral side of cartilages (Fig. 8A, C).

Superfamily Littorinoidea
Family Littorinidae

Littorina brevicula (Philippi, 1844)
(Figs. 1E, 9A, B)

Odontophore containing single unfused pair of cartilages (oc: Figs. 1E, 9A), consisting of thin matrix (m), cartilage cells (cc), large nuclei

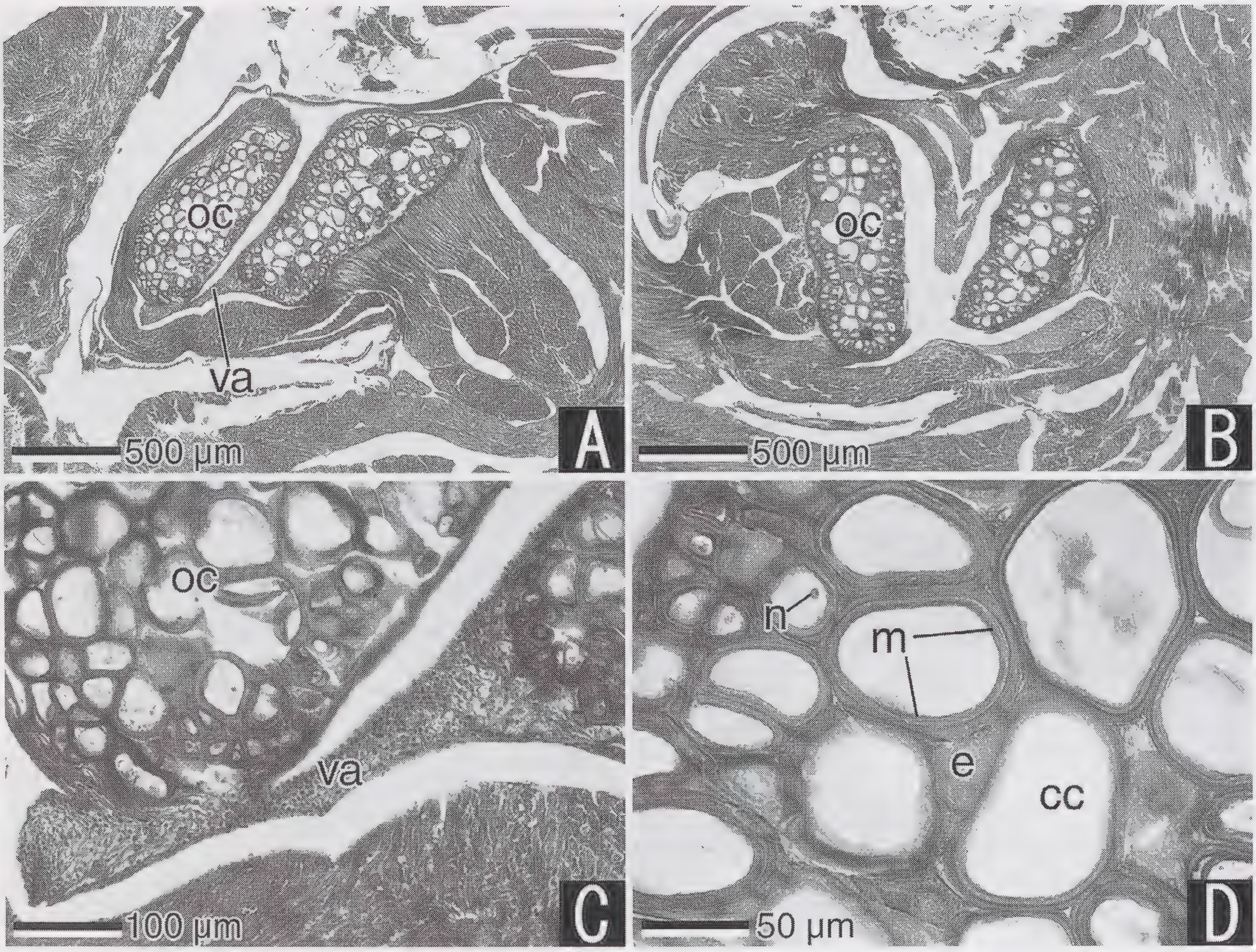

FIG. 8. Cross sections of buccal mass and odontophoral cartilages of *Cypraea boivinii* (Cypraeidae). A: Anterior part of odontophoral cartilage; B: Posterior part of odontophoral cartilage; C: Ventral approximator muscle; D: Enlarged view of odontophoral cartilage.

(n) in variable positions within cartilage cells (Fig. 9B). Cartilages closest ventrally, connected by ventral approximator muscle (va) inserting at outer lateral sides of cartilages (Fig. 9A, B). Left cartilage overlying right cartilage (Fig. 9A).

Superfamily Naticoidea
Family Naticidae

Glossaulax didyma (Röding, 1798)
(Fig. 9C, D)

Odontophore containing single unfused pair of cartilages (oc) consisting of thin matrix (m), cartilage cells (cc), and large nuclei (n) occurring in variable positions within cells (Fig. 9D). Cytoplasm of some cartilage cells stained in mazenda (Fig. 9D). Cartilages lying closest dorsally; right cartilage overlying left one (Fig. 9C). Ventral approximator muscle not clearly identified.

Superfamily Rissooidea
Family Assimineidae

Assiminea japonica Martens, 1877
(Fig. 10A, B)

Odontophore containing single unfused pair of cartilages (oc: Fig. 10A), consisting of thin matrix (m), cartilage cells (cc) with large nuclei (n) attached tightly to matrix (Fig. 10B). Matrix and cartilage cells stained in blue and faintly in mazenda, respectively. Paired cartilages closest ventrally, without overlapping. Connection between cartilages not observed.

Superfamily Stromboidea
Family Strombidae

Strombus luhuanus Linnaeus, 1758
(Fig. 10C, D)

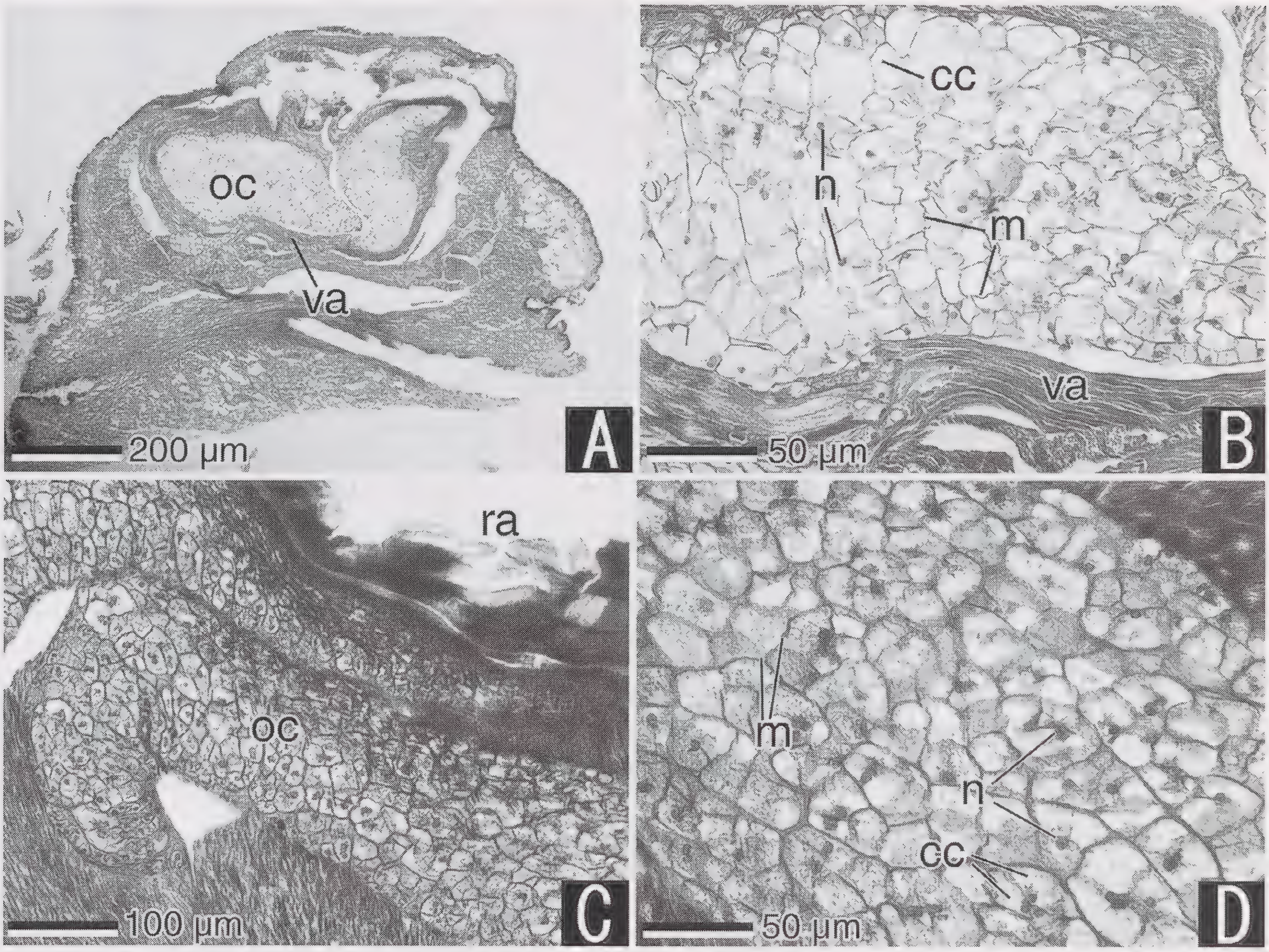

FIG. 9. Cross sections of buccal mass and odontophoral cartilages. A, B. *Littorina brevicula* (Littorinidae). A: Middle part of buccal mass; B: Enlarged view of odontophoral cartilage; C, D. *Glossaulax didyma* (Naticidae). C: Middle part of odontophoral cartilage; D: Enlarged view of odontophoral cartilage.

Odontophore containing single pair of unfused cartilages (oc), composed of thin matrix (m), cartilage cells (cc), and large nuclei (n) distributed in variable positions in cartilage cells (Fig. 10D). Cartilages closest dorsally in cross section. Ventral approximator muscle not found. Left cartilage overlying right one.

Superfamily Tonnoidea
Family Ranellidae

Fusitriton oregonensis (Redfield, 1846)
(Fig. 11)

Odontophore containing single unfused pair of cartilages (oc: Fig. 11A, B), consisting of thin matrix (m), cartilage cells (cc) with large nuclei (n) in variable positions in cells (Fig. 11D). Pair of cartilages closest ventrally, connected by ventral approximator muscle (va) inserting at inner medial side of cartilages (Fig. 11C). Left cartilage overlying right cartilage (Fig. 11A, B).

Superfamily Vanikoroidea
Family Hipponicidae

Hipponix conica (Schumacher, 1817)
(Fig. 12A, B)

Odontophore containing single unfused pair of cartilages (oc: Fig. 12A), consisting of thin matrix (m), cartilage cells (cc) with large nuclei (n) located on interior wall of matrix (Fig. 12B). Cartilages closest on dorsal side; left cartilage underlying right one (Fig. 12A). Ventral approximator muscle not found.

Superfamily Vermetoidea
Family Vermetidae

Serpulorbis imbricatus (Dunker, 1860)
(Fig. 12C, D)

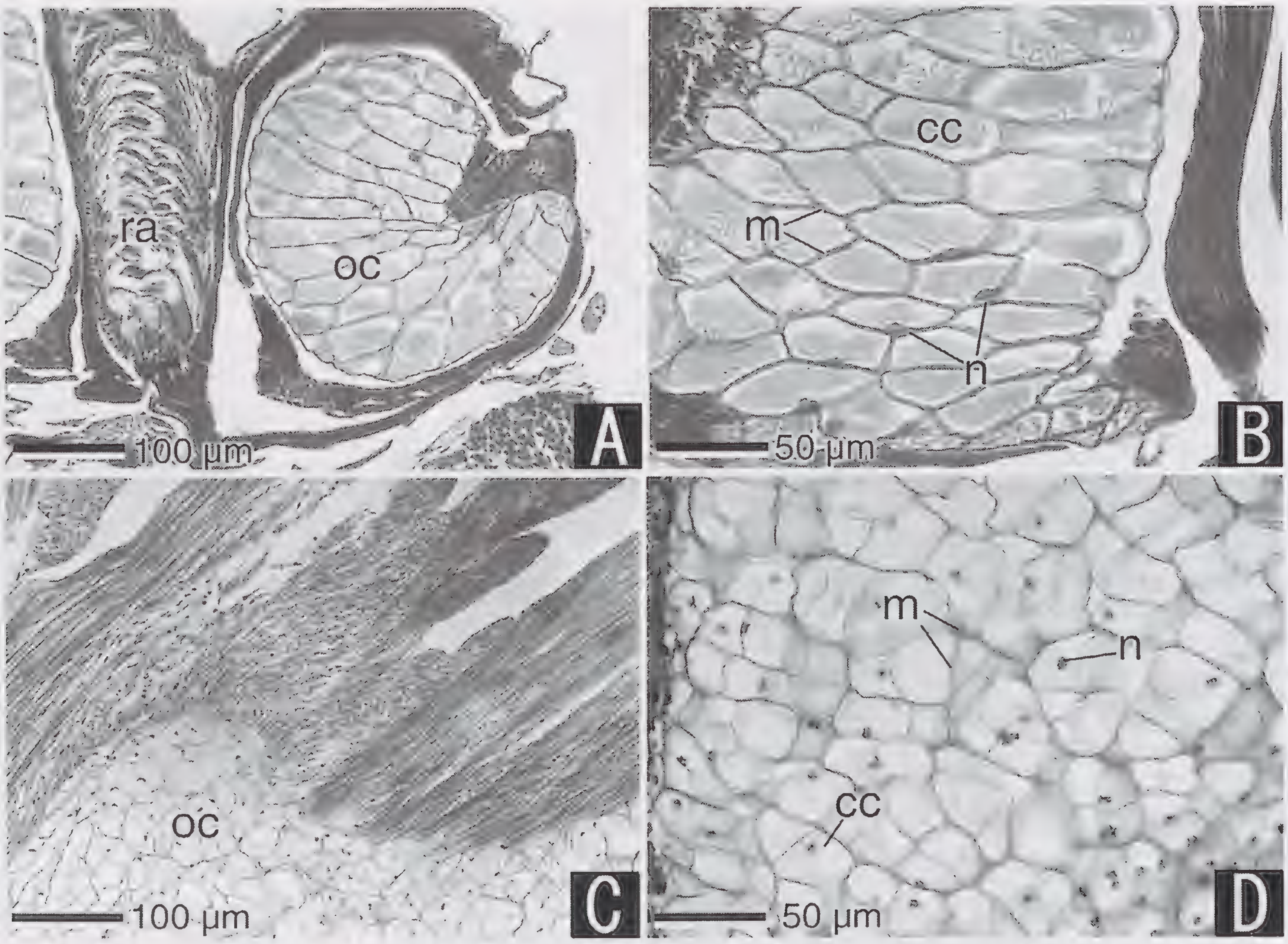

FIG. 10. Cross sections of odontophoral cartilages. A, B. *Assiminea japonica* (Assimineidae). A: Posterior part of odontophoral cartilage; B: Enlarged view of odontophoral cartilage; C, D: *Strombus luhuanus* (Strombidae); C: Odontophoral cartilage and surrounding muscle; D: Enlarged view of odontophoral cartilage.

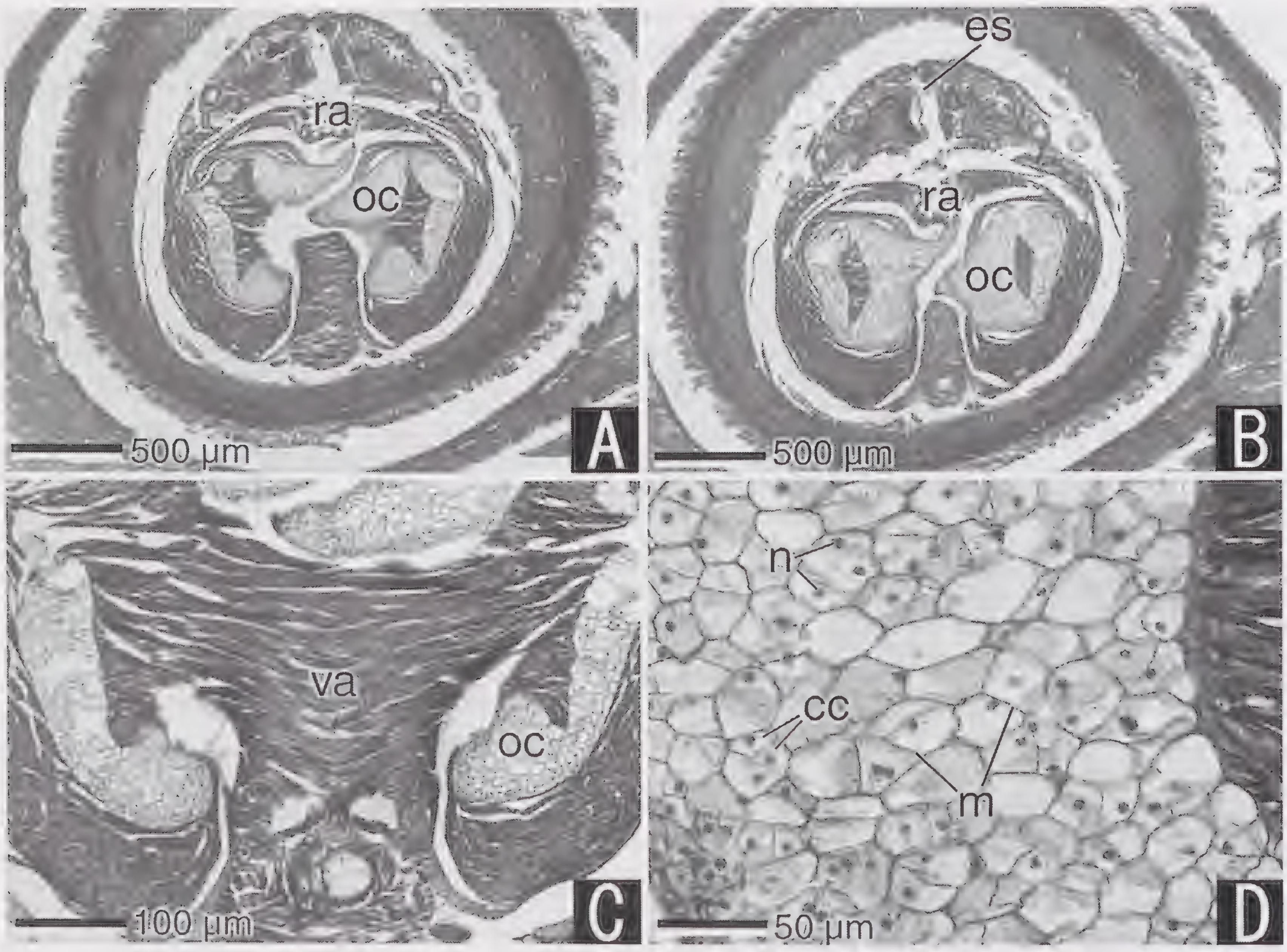

FIG. 11. Cross sections of buccal mass and odontophoral cartilage of *Fusitriton oregonensis* (Ranellidae). A: Anterior middle part of buccal mass; B: Posterior middle part of buccal mass; C: Tissue of ventral approximator muscle; D: Enlarged view of odontophoral cartilage.

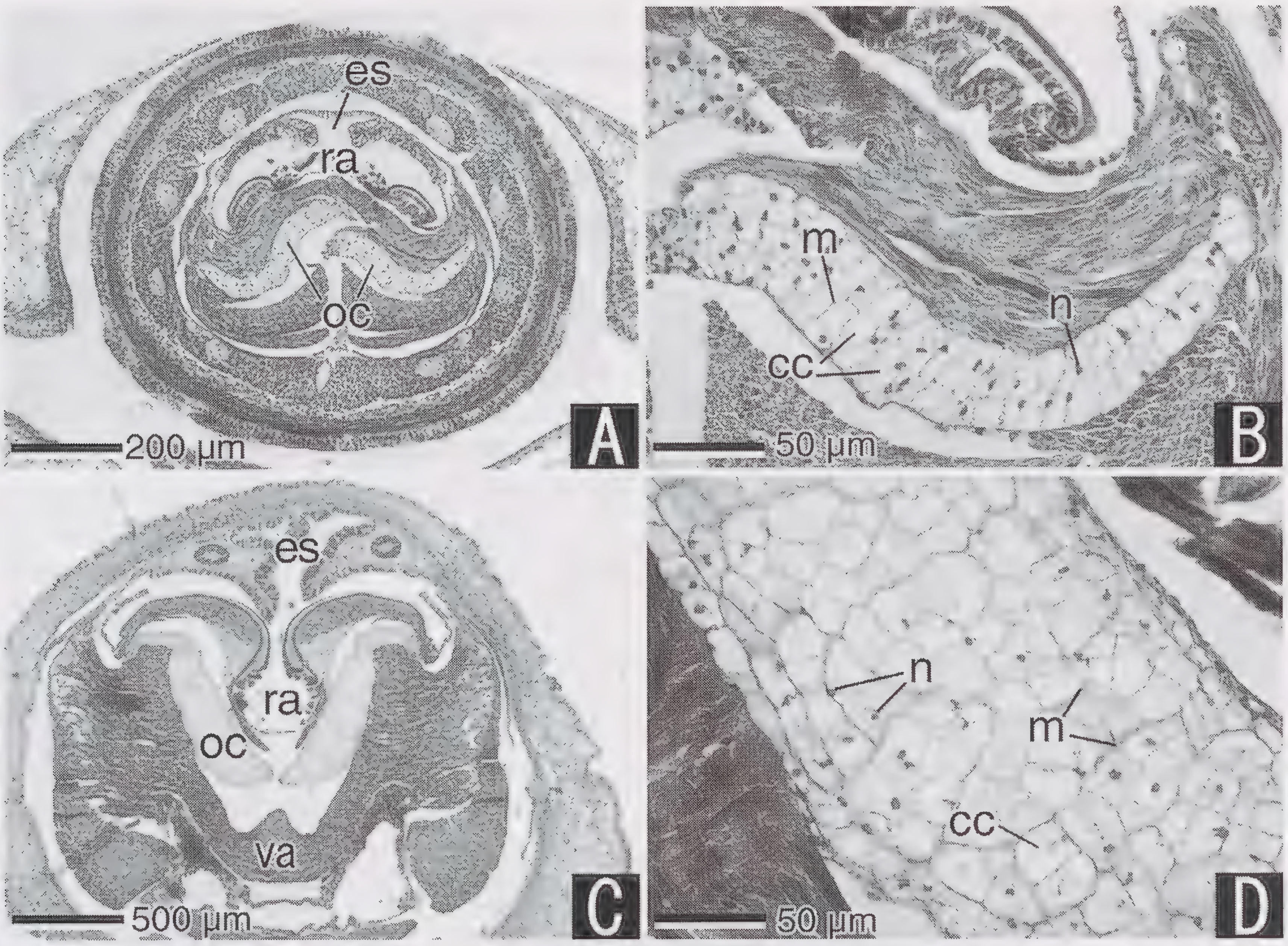

FIG. 12. Cross sections of buccal mass and odontophoral cartilages. A, B. *Hipponix conica* (Hipponicidae; A, B). A: Middle part of buccal mass; B: Enlarged view of odontophoral cartilage; C, D. *Serpulorbis imbricatus* (Vermetidae). C: Middle part of buccal mass; D: Enlarged view of odontophoral cartilage.

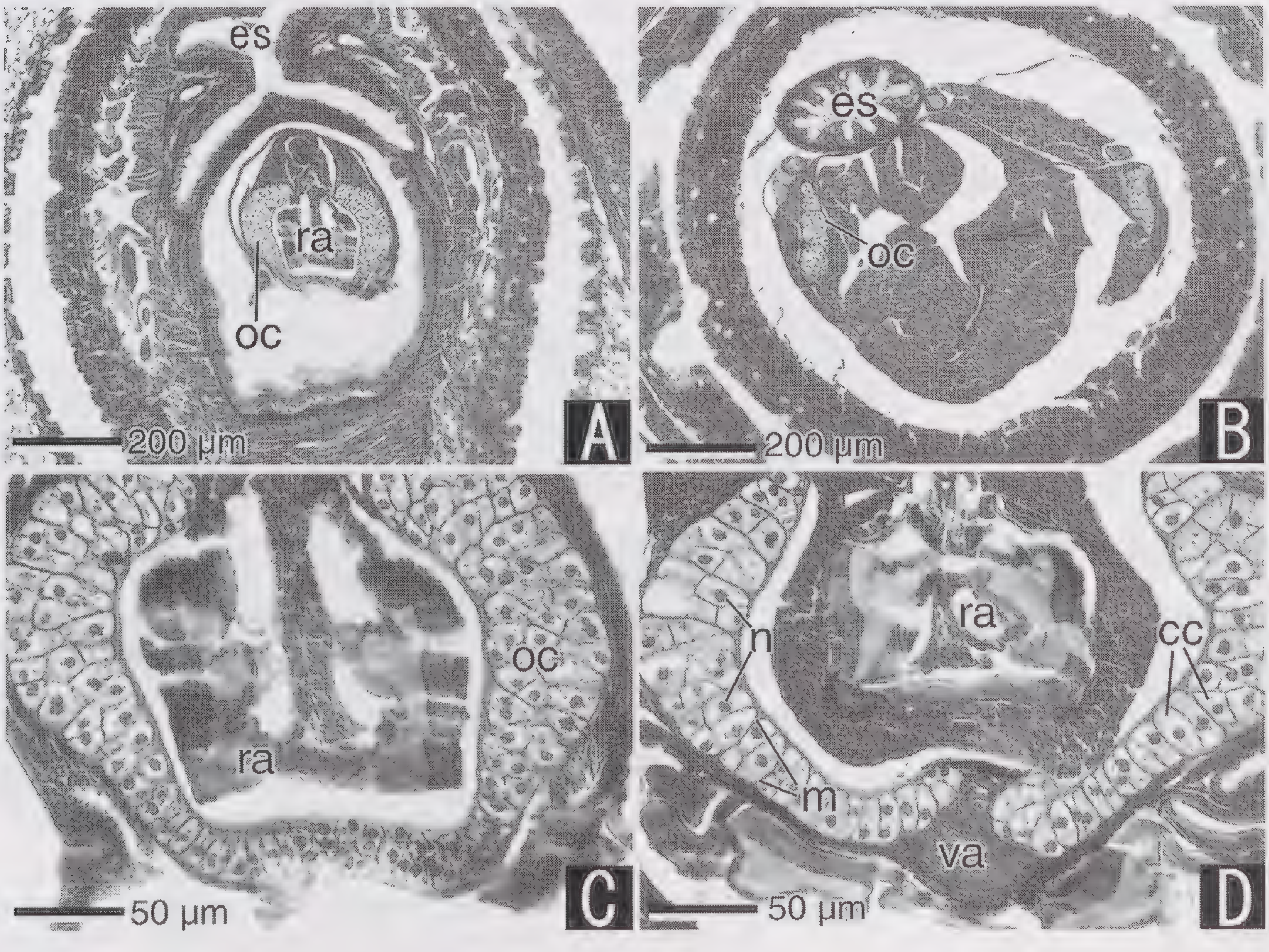

FIG. 13. Cross sections of buccal mass and odontophoral cartilages of *Japeuthria ferrea* (Buccinidae). A: Anterior part of buccal mass; B: Posterior part of buccal mass; C: Anterior end of odontophoral cartilage; D: Anterior part of odontophoral cartilages with ventral approximator muscle.

Odontophore containing single pair of unfused cartilages (oc: Fig. 12C), thin matrix (m), cartilage cells (cc), large nuclei (n) in variable positions within cartilage cells (Fig. 12D). Cartilages closest ventrally, connected by ventral approximator (va) muscle inserting at outer lateral side of cartilages (Fig. 12C). Left cartilage overlying right cartilage anteriorly.

Clade Neogastropoda
Superfamily Buccinoidea
Family Buccinidae

Japeuthria ferrea (Reeve, 1847)
(Fig. 13)

Odontophore containing one fused pair of cartilage (oc: Fig. 13A, B), consisting of thick matrix (m), cartilage cells (cc), large nuclei (n) that tend to be located in middle of cells (Fig. 13C, D). Cartilage U-shaped, symmetrical, connected anteriorly between right and left (Fig. 13A, C). In posterior area, branches of cartilage separate, connected ventrally by ventral approximator muscle (va) inserting at ventral side of cartilage (Fig. 13D). Right and left elements not overlapping each other.

Family Columbellidae

Euplica scripta (Lamarck, 1822)
(Fig. 14)

Odontophore containing single pair of cartilages (oc) fused anteriorly but separated into right and left branches posteriorly without overlapping (Fig. 14A, B), composed of thick matrix (m), cartilage cells (cc), and large nuclei (n) situated centrally within cells (Fig. 14C). Right and left branches of cartilage connected by ventral approximator muscle (va) inserting at ventral area of cartilages (Fig. 14B, D).

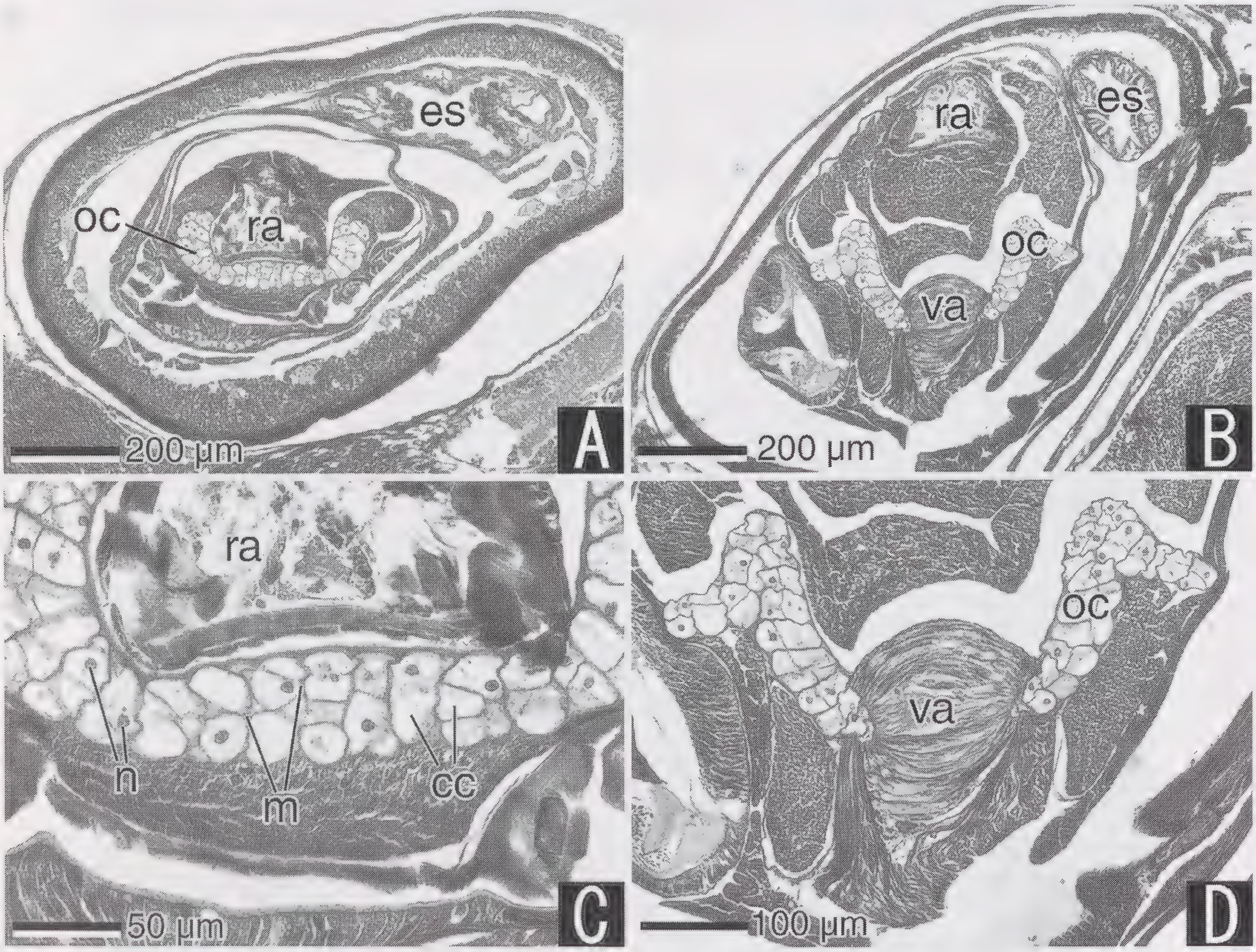

FIG. 14. Cross sections of buccal mass and odontophoral cartilages of *Euplica scripta* (Columbellidae). A: Anterior part of buccal mass; B: Middle part of buccal mass; C: Enlarged view of odontophoral cartilage; D: Middle part of anterior cartilage and ventral approximator muscle.

Family Nassariidae

Nassarius festiva (Powys, 1833)
(Fig. 15)

Odontophore containing single pair of cartilages fused anteriorly (oc: Fig. 15A) but separated posteriorly without overlapping (Fig. 15B, C). Histologically cartilage consisting of thick matrix (m), cartilage cells (cc), and large nuclei (n) located centrally within cells (Fig. 15D). Right and left elements of cartilage connected by ventral approximator muscle (va) inserting at ventral side of cartilages (Fig. 15B, D).

Superfamily Muricoidea
Family Muricidae

Thais clavigera (Küster, 1860)
(Figs. 1H, 16A–D)

Odontophore containing single cartilage (oc) which consists of two extremely elongate branches fused anteroventrally (Figs. 1H, 16C), strikingly curved outwards without overlapping (Fig. 1H). Tissue of cartilages composed of thick matrix (m), cartilage cells (cc), and large nuclei (n) situated centrally within cartilage cells (Fig. 16C, D). Right and left elements of cartilage connected by ventral approximator muscle (va) inserting at ventral area of cartilage (Fig. 16A, D).

Family Mitridae

Strigatella zebra (Lamarck, 1811)
(Figs. 1I, 16E, F)

Odontophore containing single unfused pair of cartilages (oc: Figs. 1I, 16E) that are

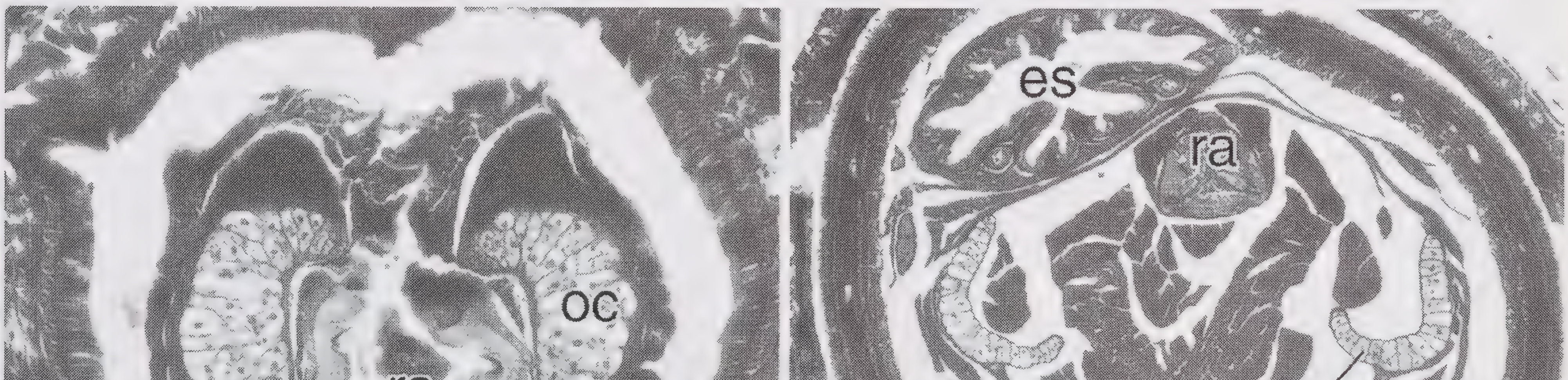

FIG. 15. Cross sections of buccal mass and odontophoral cartilages of *Nassarius festiva* (Nassariidae). A: Anterior end of odontophoral cartilage; B: Posterior middle part of buccal mass; C: Posterior part of buccal mass; D: Enlarged view of odontophoral cartilage.

composed of thick extracellular matrix (m), cartilage cells (cc) and large nuclei (n) tending to occur in center of cartilage cells (Fig. 16F). Pair of cartilages closest ventrally without overlapping (Fig. 16E), connected by ventral approximator muscle (va) inserting at ventral area (Fig. 16F).

Superfamily Conoidea
Family Conidae

Conus ebraeus Linnaeus, 1758

Buccal mass present as muscular bulb at base of proboscis, but odontophoral cartilage absent.

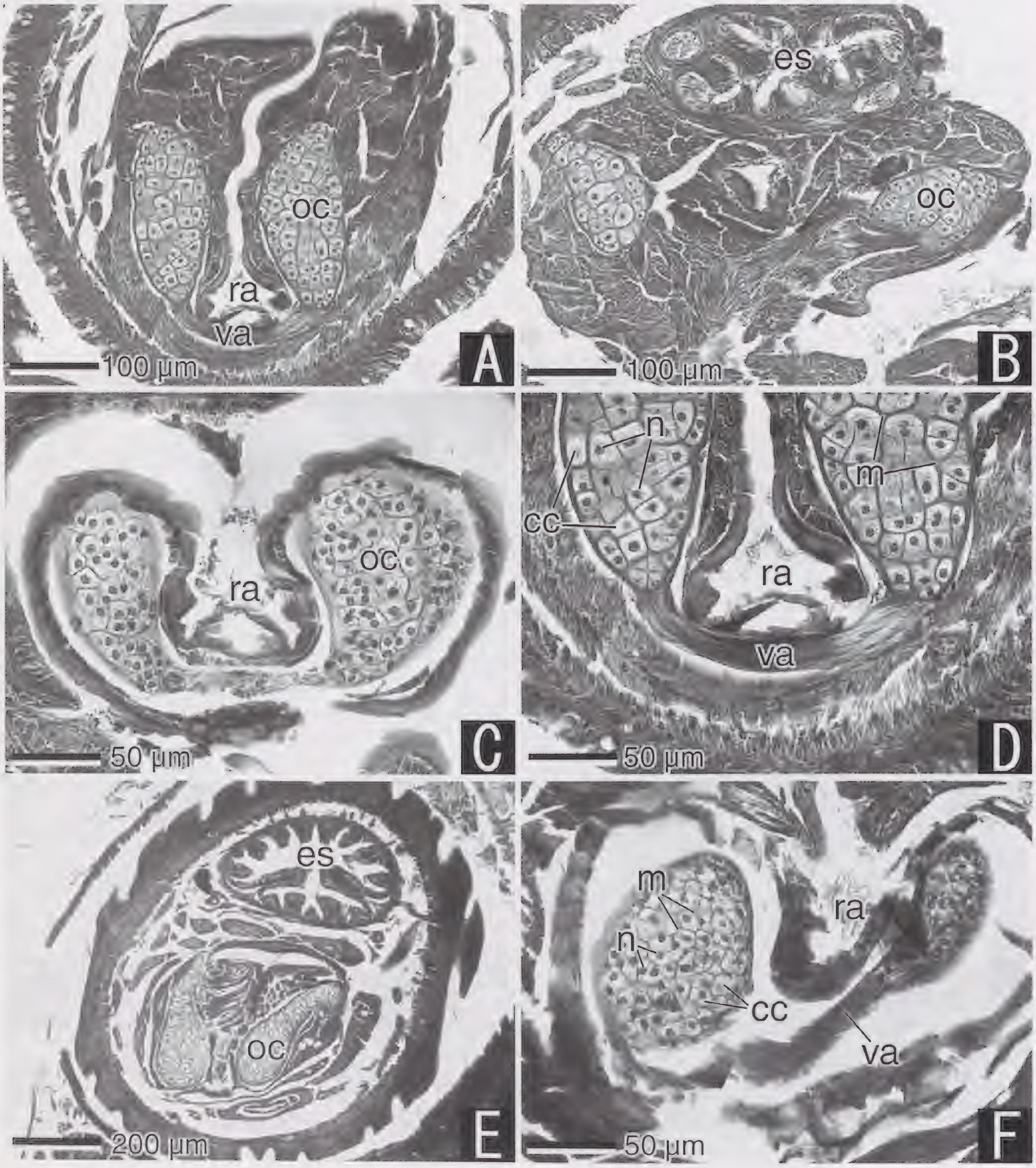

FIG. 16. Cross sections of buccal mass and odontophoral cartilages. A–D. *Thais clavigera* (Muricidae). A: Middle part of buccal mass; B: Posterior part of buccal mass; C: Anterior end of odontophoral cartilages; D: Enlarged view of odontophoral cartilages and ventral approximator muscle; E, F. *Strigatella zebra* (Mitridae). E: Middle part of buccal mass; F: Enlarged view of odontophoral cartilages and ventral approximator muscle.

Clade Heterobranchia
Informal group Opisthobranchia
Clade Cephalaspidea
Superfamily Haminoeoidea
Family Haminoeidae

Haloa japonica (Pilsbry, 1895)
(Fig. 17A, B)

Odontophore lacking cartilage or membrane-enclosed radular bolster (Fig. 17A; see Figs.

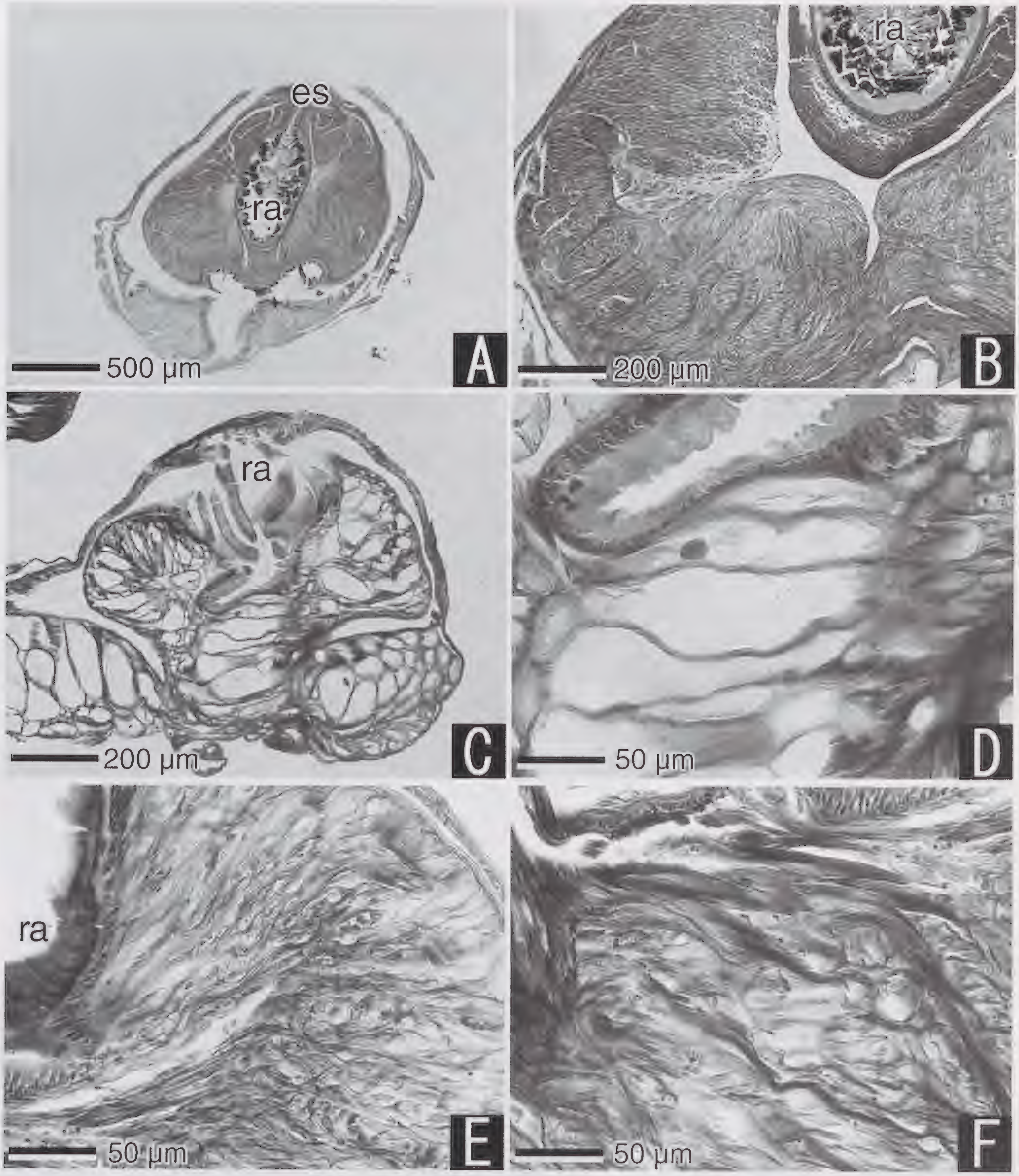

FIG. 17. Cross sections of buccal mass. A, B. *Haloa japonica* (Haminoeidae). A: Posterior part of buccal mass; B: Enlarged view of radular bolster; C, D. *Philine argentata* (Philinidae). C: Anterior part of buccal mass; D: Enlarged view of part of Fig. 17A; E, F. *Nipponoscaphander japonica* (Cylichnidae). E, F: Enlarged view of connective tissue and muscle fibers in radular bolster.

19–22 for comparison), densely filled with fibrous connective tissue and muscle fibers arranged in variable directions (Fig. 17B). Ventral approximator muscle not observed.

Superfamily Philinoidea
Family Philinidae

Philine argentata Gould, 1859
(Fig. 17C, D)

Odontophore lacking true cartilage or membrane-enclosed radular bolster (Fig. 17C), filled with loosely organized network-like structure (Fig. 17D), being composed of fibrous

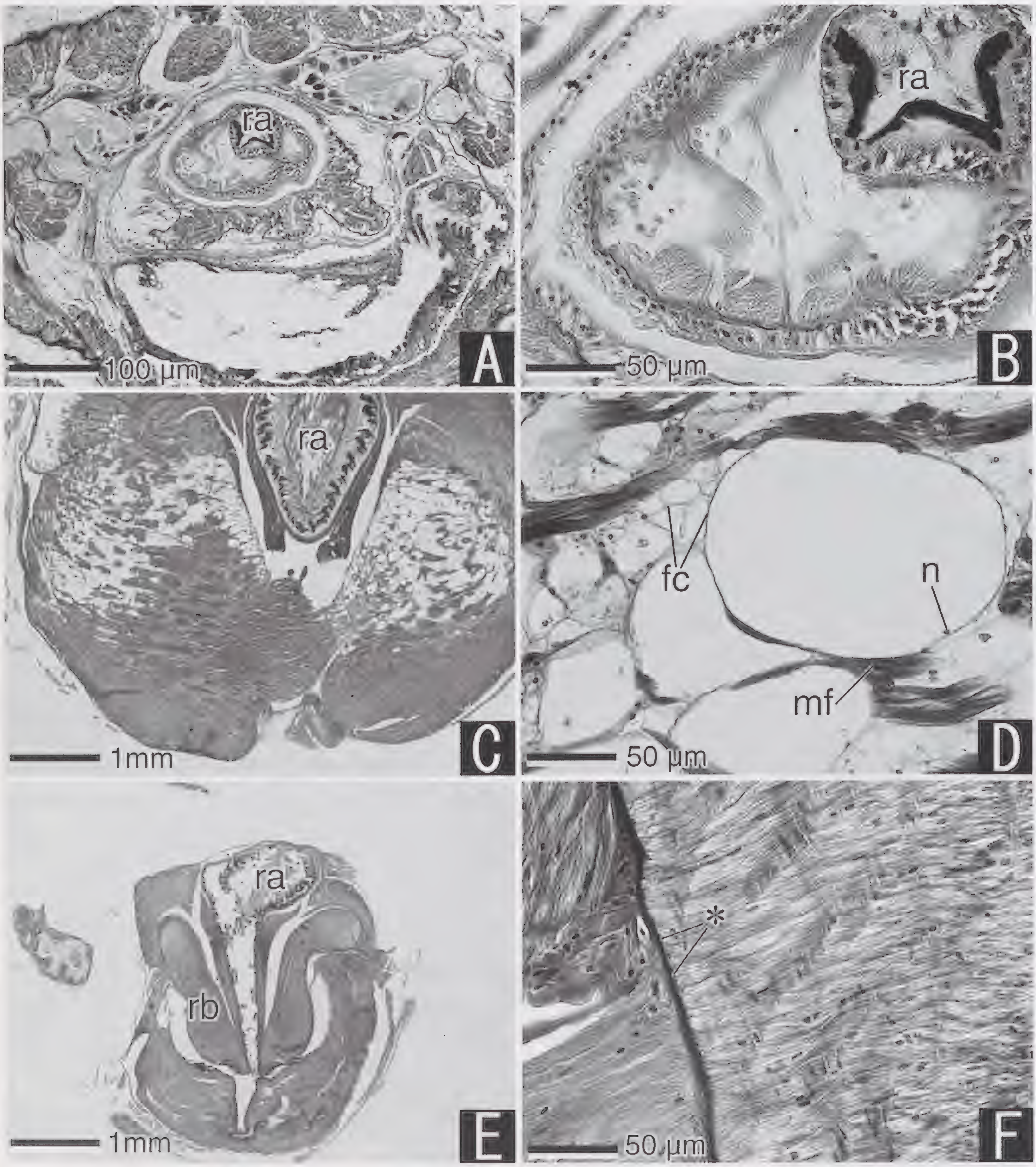

FIG. 18. Cross sections of buccal mass. A, B: *Cavolinia uncinata* (Cavoliniidae). A: Middle part of buccal mass; B: Enlarged view of part of Fig. 18A; C, D. *Aplysia oculifera* (Aplysiidae). C: Middle part of buccal mass; D: Enlarged view of connective tissue and muscle fibers in radular bolster; E, F. *Hypselodoris festiva* (Chromodorididae). E: Middle part of buccal mass; F: Enlarged view of radular bolster (right) and surrounding muscles (left) separated by a sheet of collagen fibers (asterisk).

connective tissue and muscle fibers. Ventral approximator muscle not identified.

Family Cylichnidae

Nipponoscaphander japonica (A. Adams, 1862)
(Fig. 17E, F)

Odontophore lacking cartilage or membrane-enclosed radular bolster, filled densely with complex of regularly radiating fibrous connective tissue and muscle fibers uniformly (Fig. 17E, F). Ventral approximator muscle not observed.

Clade Thecosomata
Superfamily Cavolinioidea
Family Cavoliniidae

Cavolinia uncinata (Rang, 1829)
(Fig. 18A, B)

Odontophore lacking cartilage or membrane-enclosed radular bolster, containing remarkably loose complex of fibrous connective tissue, filled internally with large space of blood sinus, surrounded exteriorly by layer of epithelial cells (Fig. 18A, B). Ventral approximator muscle not identified.

Clade Aplysiomorpha
Superfamily Aplysioidea
Family Aplysiidae

Aplysia oculifera A. Adams & Reeve, 1850
(Fig. 18C, D)

Odontophore lacking true cartilaginous tissue (Fig. 18C), filled with complex of fibrous connective tissue (fc) and muscle fibers (mf). Middle portion of radular bolsters occupied by bubble-shaped spaces of variable size, small granular nuclei (n) widely scattered in fibrous connective tissue (Fig. 18D). Dorsal and ven-

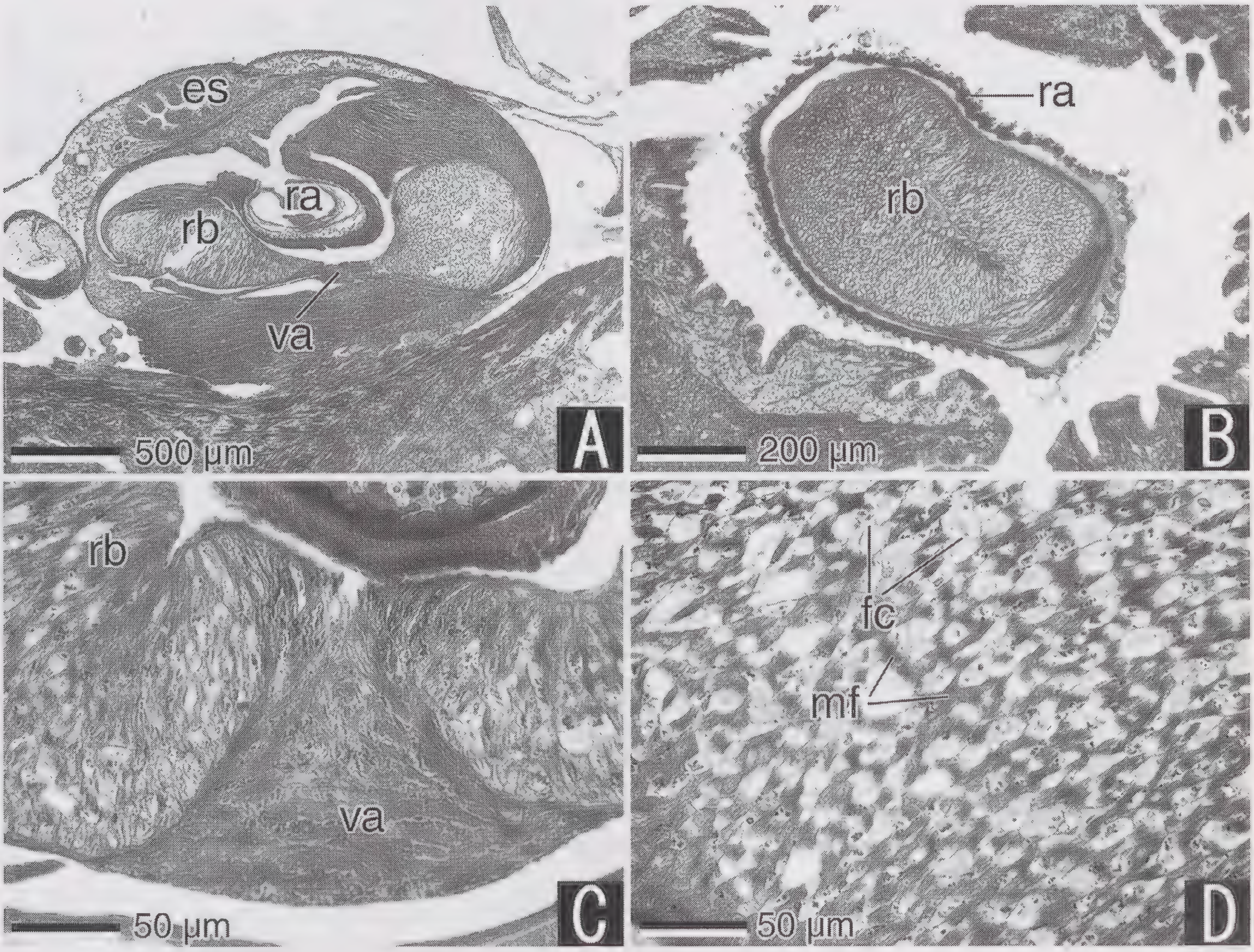

FIG. 19. Cross sections of buccal mass and radular bolsters of *Siphonaria japonica* (Siphonariidae). A: Middle part of buccal mass; B: Anterior end of radular bolster; C: Middle part of radular bolsters connected by ventral approximator muscle (va); D: Enlarged view of radular bolster.

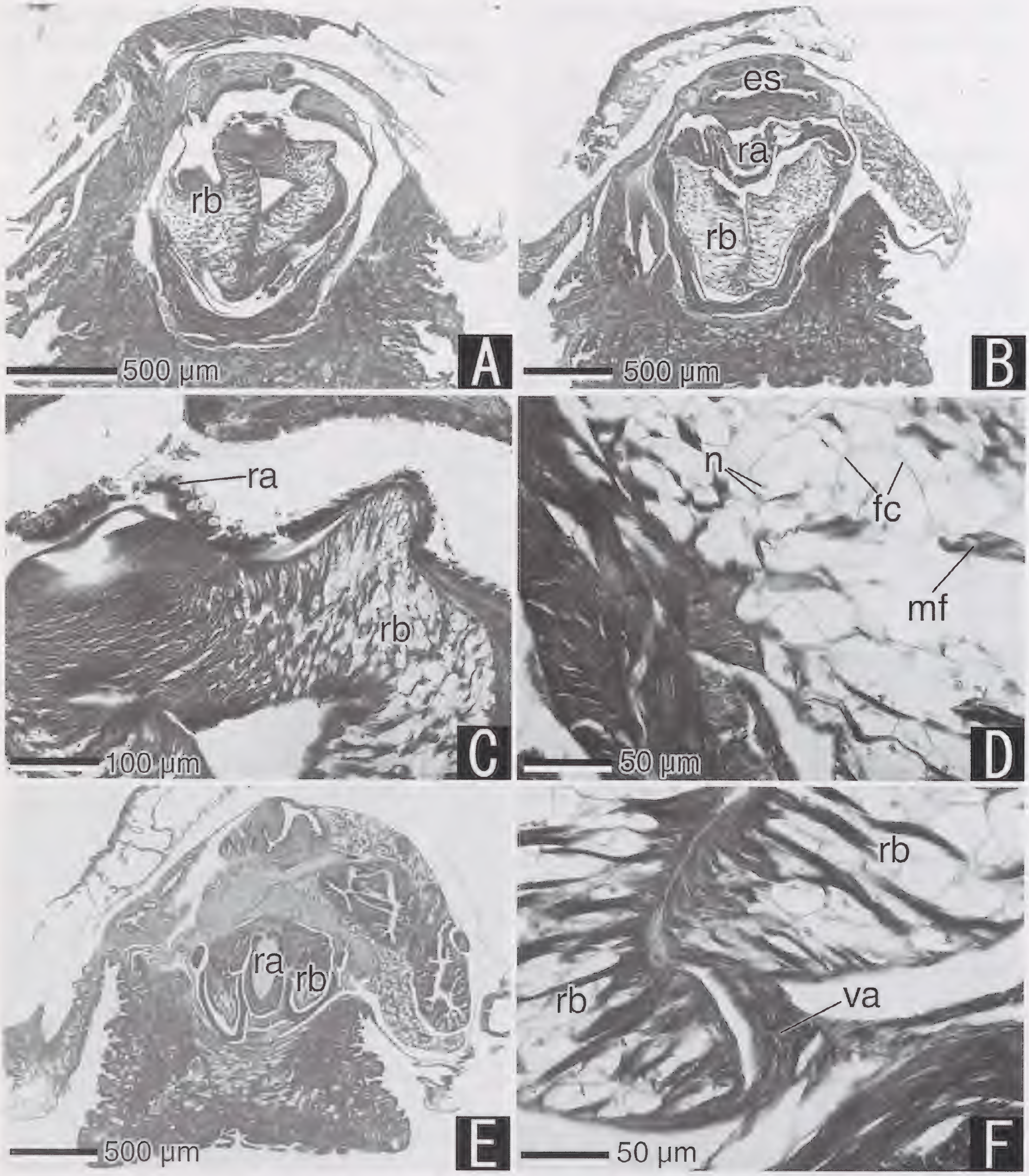

FIG. 20. Cross sections of buccal mass and radular bolsters of *Lymnaea stagnalis* (Lymnaeidae). A: Anterior part of buccal mass; B: Middle part of buccal mass; C: Anterior part of radular bolster; D: Enlarged view of radular bolster; E: Posterior part of buccal mass; F: Connection between ventral approximator muscle and radular bolster.

tral portions of radular bolsters lacking bubble-like tissue and densely packed with connective and muscular tissue. Ventral approximator muscle not observed.

Clade Euctenidiacea
Subclade Doridacea
Superfamily Doridoidea
Family Chromodorididae

Hypselodoris festiva (A. Adams, 1861)
(Fig. 18E, F)

Odontophore containing paired stiffened radular bolsters (rb: Fig. 18E) enwrapped by thin fibrous layer (asterisk in Fig. 18F), sharply separated from other buccal musculature, but fused with radular retractor muscle ventrally (Fig. 18E). Radular bolsters filled with densely packed fibers (Fig. 18F). Ventral approximator muscle not identified.

Informal group Pulmonata
Informal group Basommatophora
Superfamily Siphonarioidea
Family Siphonariidae

Siphonaria japonica (Donovan, 1824)
(Fig. 19)

Odontophore containing fused pair of radular bolsters (rb: Fig. 19A), not containing cartilage-like structure. Histologically radular bolsters consisting of variously oriented mixture of fibrous connective tissue (fc), muscle fibers (mc), darkly stained granular nuclei, densely scattered small transparent spaces that were not stained by Azan method.

Right and left elements of radular bolsters fused in anterior end (Fig. 19B), closest ventrally without overlapping in cross section (Fig. 19A), connected by ventral approximator muscle (va) inserting at ventral area of radular bolsters (Fig. 19C). Radular bolsters separated from surrounding buccal musculature by membrane (Fig. 19A).

Clade Hygrophila
Superfamily Lymnaeoidea
Family Lymnaeidae

Lymnaea stagnalis (Linnaeus, 1758)
(Fig. 20)

Odontophore containing fused pair of radular bolsters (rb: Fig. 20B) which are composed

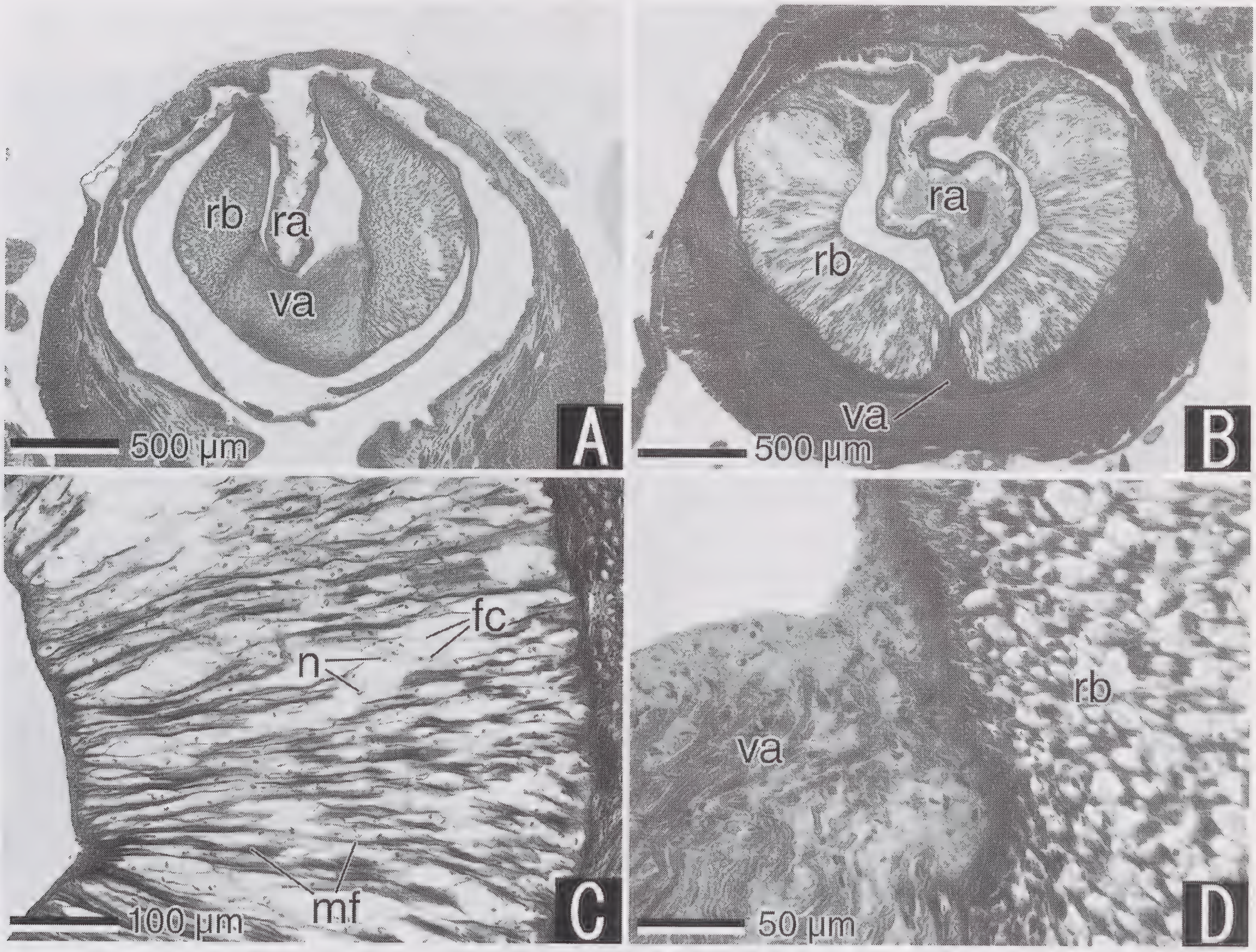

FIG. 21. Cross sections of buccal mass and radular bolster of *Peronia* sp. cf. *verruculatum* (Onchidiidae). A: Anterior end of buccal mass; B: Middle part of buccal mass; C: Enlarged view of radular bolster; D: Connection between ventral approximator muscle and radular bolster.

histologically of loose fibrous connective tissue (fc) and muscle fibers (mf) (Fig. 20D). Cartilage matrix absent. Right and left elements of radular bolster fused at anterior end (Fig. 20A, C), closest ventrally without overlapping, and connected by ventral approximator muscle (va) inserting at ventral side (Fig. 20B). Tissue of radular bolsters not merged with outer buccal musculatures by its enclosing membrane (Fig. 20A, B).

Clade Eupulmonata
Clade Systellommatophora
Superfamily Onchidioidea
Family Onchidiidae

Peronia sp. cf. *verruculatum* (Cuvier, 1830)
(Figs. 1J, 21)

Odontophore containing unfused pair of radular bolsters (rb: Figs. 1J, 21A, B) consisting of fibrous connective tissue (fc) and muscle fibers (mf: Fig. 21C). Cartilage matrix absent. Pair of radular bolsters closest ventrally without overlapping and connected by single layer of ventral approximator muscle (va: Fig. 21D). Ventral approximator muscle inserting at ventral area of radular bolsters (Fig. 21A, B). Radular bolsters clearly delimited from outer buccal musculature by membrane (Fig. 21B).

Clade Stylommatophora
Informal group Sigmurethra
Superfamily Helicoidea
Family Bradybaenidae

Acusta despecta sieboldiana (Pfeiffer, 1850)
(Figs. 1K, 22)

Odontophore containing fused paired radular bolster (rb: Figs. 1K, 22A), composed of condensed fibrous connective tissue and muscle fibers (Fig. 22D). Cartilage matrix absent. Right and left elements of radular bolster fused at anterior end, closest ventrally without overlapping in cross section (Fig. 22C), and connected by ventral approximator muscle (va) on ventral side (Fig. 22C). Radular bolster sharply delimited from surrounding buccal musculature by membrane (Fig. 22C).

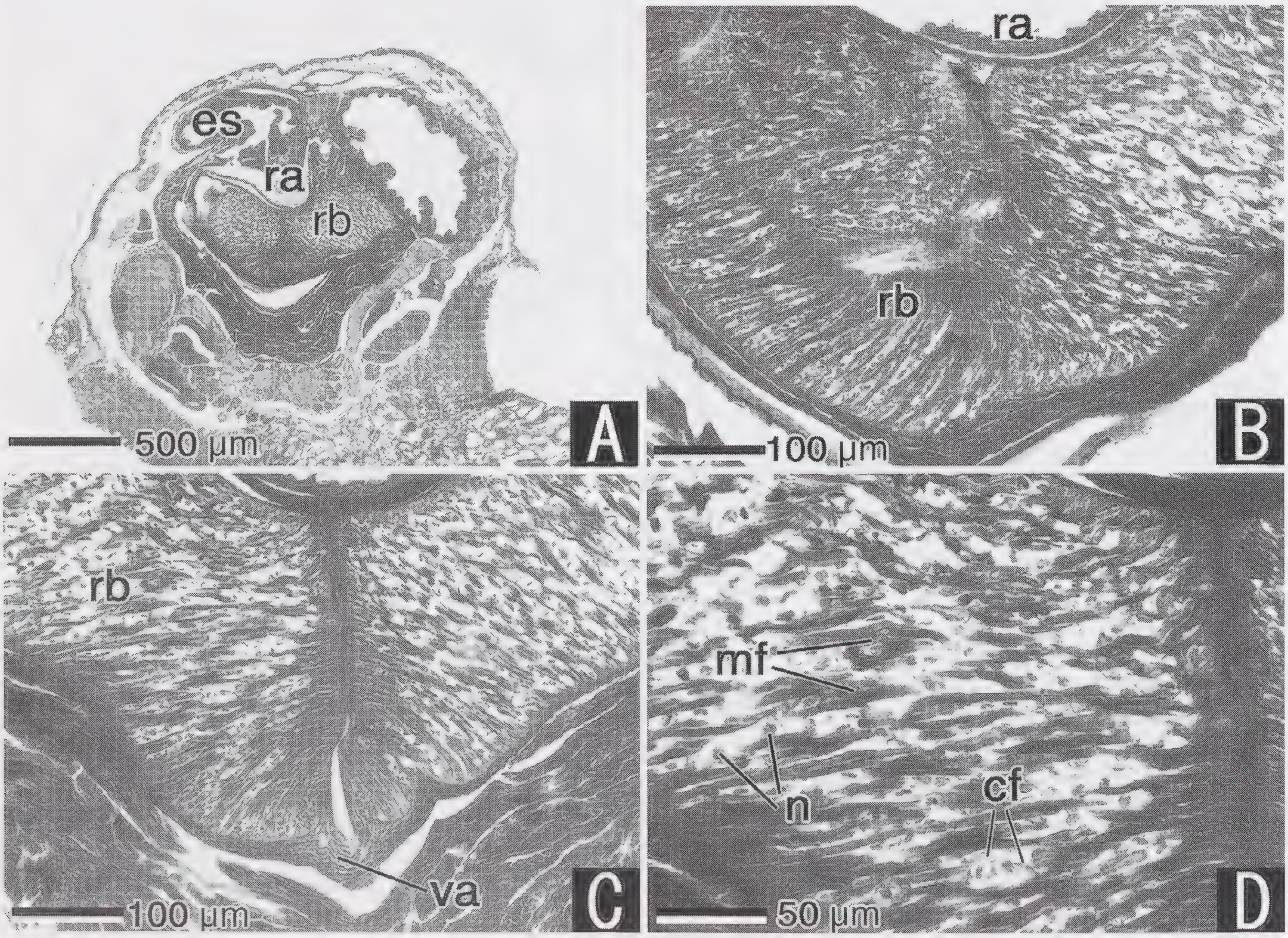

FIG. 22. Cross sections of buccal mass and radular bolsters of *Acusta despecta sieboldiana* (Bradybaenidae). A: Anterior end of buccal mass; B: Anterior end radular bolster; C: Connection between ventral approximator muscle (va) and radular bolster (rb); D: Enlarged view of radular bolster.

TABLE 2. Taxonomic distribution of odontophoral cartilages or radular bolsters. ++ = present in all species examined; + = present in part; - = absent. Co: Cocculinoidea, He: Heterobranchia, Ng: Neogastropoda, Ne: Neritimorpha, Pa: Patellogastropoda, tC: taenioglossate Caenogastropoda, Ve: Vetigastropoda. See caption of Appendix for abbreviations of cartilages.
*Anterior cartilage is type 1, and median cartilage is type 3.
**Dorsal layer originating from medial side, and ventral layer from ventral side.

		Pa	Ve	Co	Ne	tC	Ng	He
Number of odontophoral cartilages or radular bolsters	0	-	-	-	-	-	+	+
	1 (fused)	-	-	-	-	-	+	+
	2	-	+	++	-	++	+	+
	4 (ac + alc)	+	-	-	-	-	-	-
	4 (ac + adc)	-	+	-	-	-	-	-
	4 (ac + pc)	-	+	-	-	-	-	-
	5	-	+	-	++	-	-	-
	6	+	-	-	-	-	-	-
	10	+	-	-	-	-	-	-
Composition of odontophoral cartilages	ac	++	++	++	++	++	++	-
	alc	++	-	-	-	-	-	-
	pc	+	+	-	++	-	-	-
	adc	-	+	-	-	-	-	-
	pdc	+	-	-	-	-	-	-
	mc	-	+	-	++	-	-	-
Histology	Type 1	++	+	-	++*	-	-	-
	Type 2	-	+	++	-	-	-	-
	Type 3	-	+	-	++*	+	-	-
	Type 4	-	-	-	-	+	-	-
	Type 5	-	-	-	-	-	+	-
	Type 6	-	-	-	-	-	-	+
Membrane enclosing cartilages or radular bolsters		++	++	++	++	++	++	+
Overlaping of right and left main cartilages or radular bolsters		-	-	-	-	+	-	-
Closest position of main cartilages or radular bolsters	ventral side	++	++	++	++	+	++	++
	dorsal side	-	-	-	-	+	-	-
Insertion of ventral approximator muscle	ventral side	+**	++	++	++	+	++	+
	medial side	+**	-	-	-	+	-	-
	outer lateral side	-	-	-	-	+	-	-
	dorsal side	-	-	-	-	-	-	-
	absent	-	-	-	-	+	-	+

DISCUSSION

Morphological Diversity

Greater morphological diversity in gastropod radula-supporting organs was revealed in this study than previously acknowledged. The characters mostly used for phylogenetic analysis are the number of cartilages and the presence or absence of the cartilages (Haszprunar 1988a: table 2; Ponder & Lindberg, 1997: character #68; Sasaki, 1998: characters #54–56; Barker, 2001: character #2; Dayrat & Tillier, 2002: character #34; Strong, 2003: character #13).

In this study, notable differences were observed in the following six characters at higher taxonomic level. Their states for each species are shown in the Appendix, and summarized for each higher taxon in Table 2.

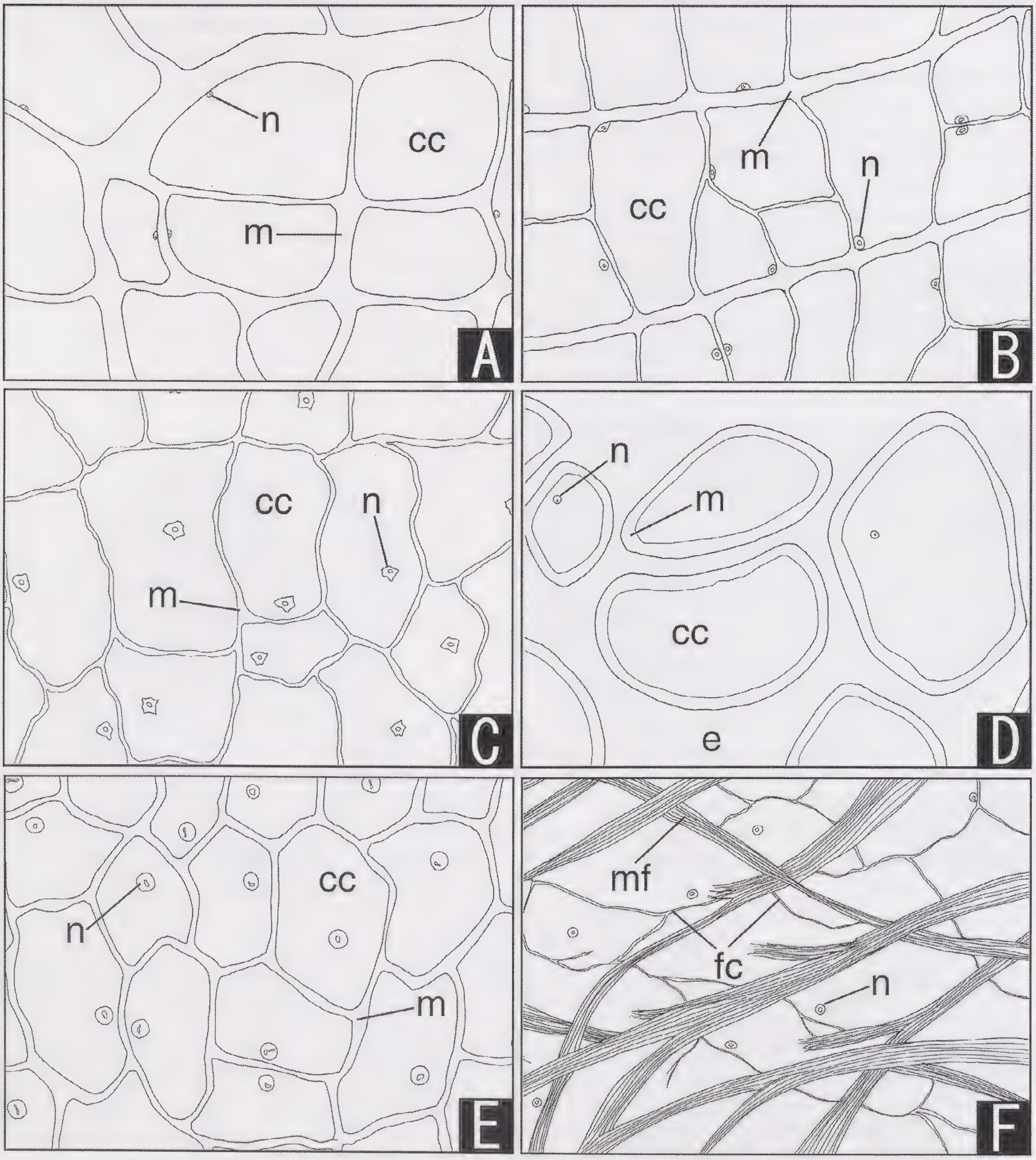

FIG. 23. Schematic diagrams of 6 types of cartilage tissue. A: Type 1; B: Type 2; C: Type 3; D: Type 4; E: Type 5; F: Type 6. (See text.)

(1) *Numbers of Odontophoral Cartilages*: In gastropods, the number of cartilages varies from a single cartilage to five pairs, or are lacking. Most commonly, there are one or two pairs. When two pairs are present, two different types can be recognized – anterior and anterolateral pairs of the Acmaeoidea (Patellogastropoda) and anterior and posterior pairs in Vetigastropoda. In the Patelloida (Patellogastropoda), there are three or more pairs of cartilages including an anterior pair. In the Neritomorpha, the number of cartilages is typically five (two pairs and an unpaired cartilage). In the apogastropod clade, there are one pair, a single fused piece or none in the Caenogastropoda, or the cartilages are replaced with muscle and connective tissue in the Heterobranchia.

In the phylum Mollusca, odontophoral cartilages or corresponding structures are present in the "Aplacophora", Monoplacophora, Polyplacophora, Scaphopoda and Gastropoda, whereas they are lacking in the Cephalopoda and Bivalvia (Salvini-Plawen, 1988; Ponder & Lindberg, 1997: 146; Messenger & Young, 1999; Table 2). The number of cartilages or cartilage-like structures is a single pair in aplacophorans (Salvini-Plawen, 1988; Scheltema et al., 1994) and Scaphopoda (Morton, 1959; Shimek & Steiner: 1997: 39–42, fig. 35), one or two pairs in Monoplacophora (Lemche & Wingstrand, 1959; Wingstrand, 1985: fig. 15; Schaefer & Haszprunar, 1996; Haszprunar & Schaefer, 1996, 1997), and two pairs in Polyplacophora (Wingstrand, 1985: fig. 15; Salvini-Plawen, 1988). The number in these outgroups suggests that one or two odontophoral cartilages or comparable structures have occurred in an ancestral group of Mollusca, conserved in various molluscan classes and subsequently increased or decreased within various groups of gastropods.

(2) *Histology*: The tissue of gastropod radular-supporting structures can be categorized into six types based on the following criteria of (a) the presence or absence of the cartilage cells surrounded by the extracellular matrix; (b) a relative thickness of the extracellular matrix around cartilage cells; (c) the relative size of the nuclei compared to the cartilage cells; and (d) the positions of the nuclei within the cartilage cells.

Type 1: The cartilage matrix is relatively thick; compared to other types of tissue, nuclei are small and tend to attach to the matrix at the edge of the cartilage cells (Fig. 23A). The size of nuclei is approximately 7 to 10% of cell length. This type is found in Patellogastropoda, Vetigastropoda, and Neritimorpha (Figs. 2–4, 5C–F).

Type 2: The cartilage is sectored by thick parallel sheets of matrix connected vertically by thin layers of matrix; the nuclei are relatively large in size and occur in various positions within the cartilage cells (Fig. 23B). The size of nuclei is around 14% of cell length. This type is observed in Cocculinidae (Fig. 5) and Lepetelloidea (Haszprunar, 1988c; Haszprunar & McLean, 1996).

Type 3: The cartilage matrix is thin and obscure in outline; nuclei are relatively large and can be located in various part of the cartilage cells (Fig. 23C). The size nuclei is approximately 9–11% of cell length. This type is frequently observed in taenioglossate Caenogastropoda (e.g., Berthold, 1991; Figs. 6, 7, 9–12).

Type 4: The cartilage matrix is markedly thick; extracellular matrix substance stained red by Heidenhain's Azan method extensively fills spaces between cartilage matricies; nuclei are small relative to cartilage cells and variously located within cartilage cells (Fig. 23D). The size of nuclei is about 5% of cell length. We have only observed this type in the caenogastropod family Cypraeidae (Fig. 8).

Type 5: Cartilage matrix is not as thick as type 1, but sharply bordered; nuclei are relatively large and tend to be located at the center of cartilage cells (Fig. 23E). The size of nuclei is between 10% and 20% of cell length. This type is characteristic of the clade Neogastropoda (Figs. 13–16).

Type 6: Cartilaginous tissue as defined above is absent; the radular bolsters are filled with muscular fibers and fibrous connective tissue which is probably composed of collagen fibres (Fig. 23F). This type was observed in all the species of Heterobranchia examined (Figs. 17–22) regardless of their radular types.

Comparison of outgroups (scaphopods and chitons; Fig. 24) suggests that the histology of the radular-supporting structures is highly diversified in non-gastropod classes. "Odontophoral cartilages" in some aplacophorans are composed mainly of muscle and collagen fiber (Scheltema et al., 1994). In Polyplacophora, the cartilages are somewhat similar to type-2 cartilages of *Cocculina* (Fig. 5B). The radular bolster tissue of

Scaphopoda is similarly composed of muscle and fibrous connective tissue (Shimek & Steiner, 1997; Fig. 24). In Monoplacophora, thin matrix and cartilage cells are observed (Haszprunar & Schaefer, 1996). Based on recent phylogenetic hypotheses of gastropods (e.g., Ponder & Lindberg, 1997; Sasaki, 1998), the primitive state of the cartilage is probably type 1, because it is widely shared by basal gastropods such as Patellogastropoda, Vetigastropoda, and Neritimorpha.

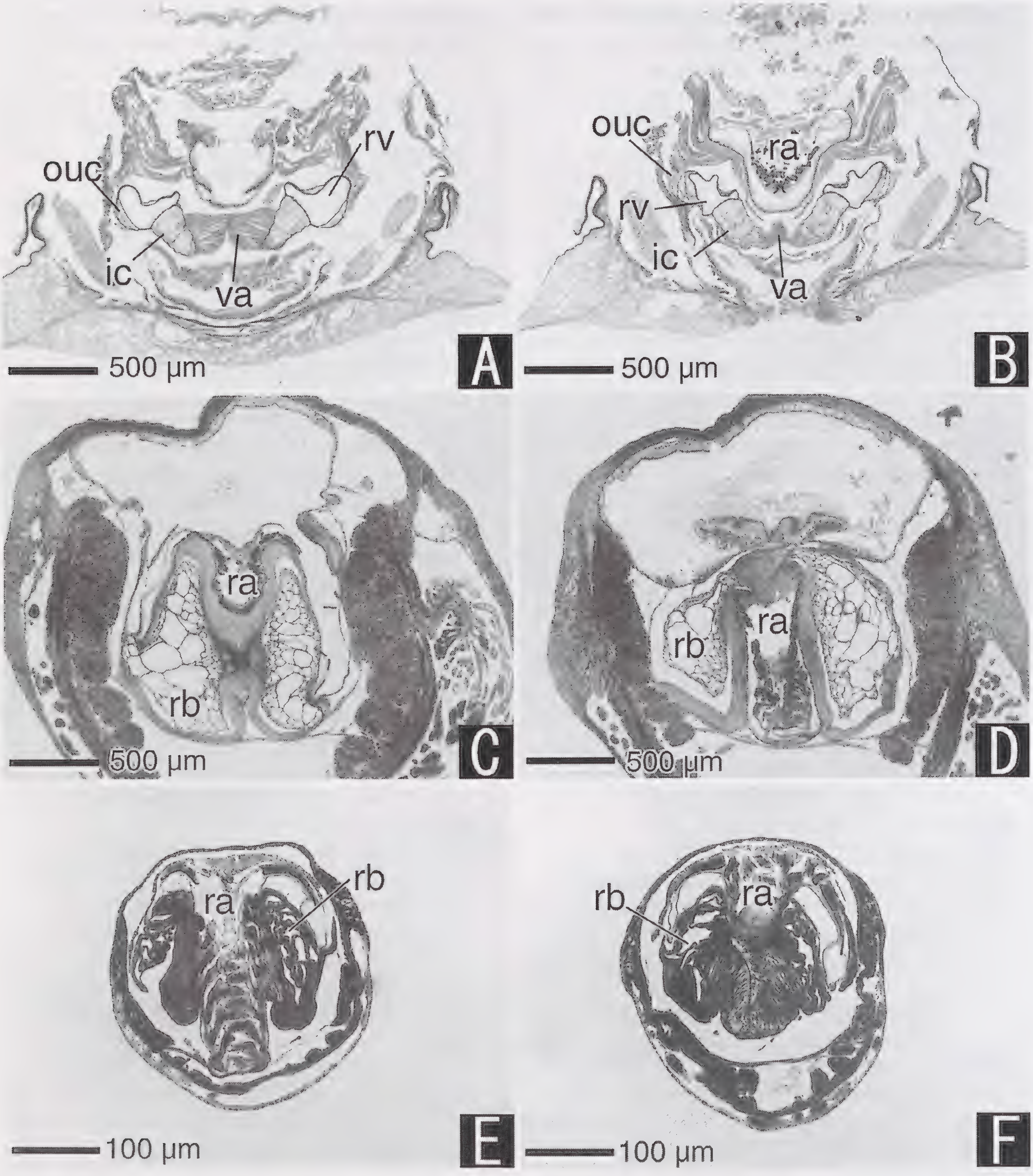

FIG. 24. Cross sections of buccal mass of non-gastropod molluscs. A, B: *Ischnochiton comptus* (Gould, 1859) (Polyplacophora: Ischnochitonidae). Anterior (A) and middle (B) part of buccal mass; C, D: *Dentalium octangulatum* Donovan, 1804 (Scaphopoda: Dentaliidae). Anterior (C) and posterior (D) part of buccal mass; E, F: *Episiphon subrectum* (Jeffreys, 1883) (Scaphopoda: Gadilinidae). Middle (E) and posterior (F) part of buccal mass.

In the species we observed, there is no clear correlation between the body size and the ratio of nuclei size to cell length (e.g., small-sized *Assiminea* vs. other larger caenogastropods).

(3) *Presence or Absence of an Enclosing Membrane*: The odontophoral cartilages or radular bolsters of molluscs are enclosed by a membrane and clearly demarcated from surrounding muscles, except some lower heterobranchs (Haminoeidae, Philinidae, Cylichnidae, Cavoliniidae, and Aplysiidae). Since the odontophoral cartilages of non-gastropods are also clearly defined, this enveloped type is considered to be primitive in Gastropoda.

(4) *Overlapping of Right and Left Main Cartilages or Radular Bolsters* (Fig. 25): The topological condition of the right and left elements (cartilages and radular bolsters) is

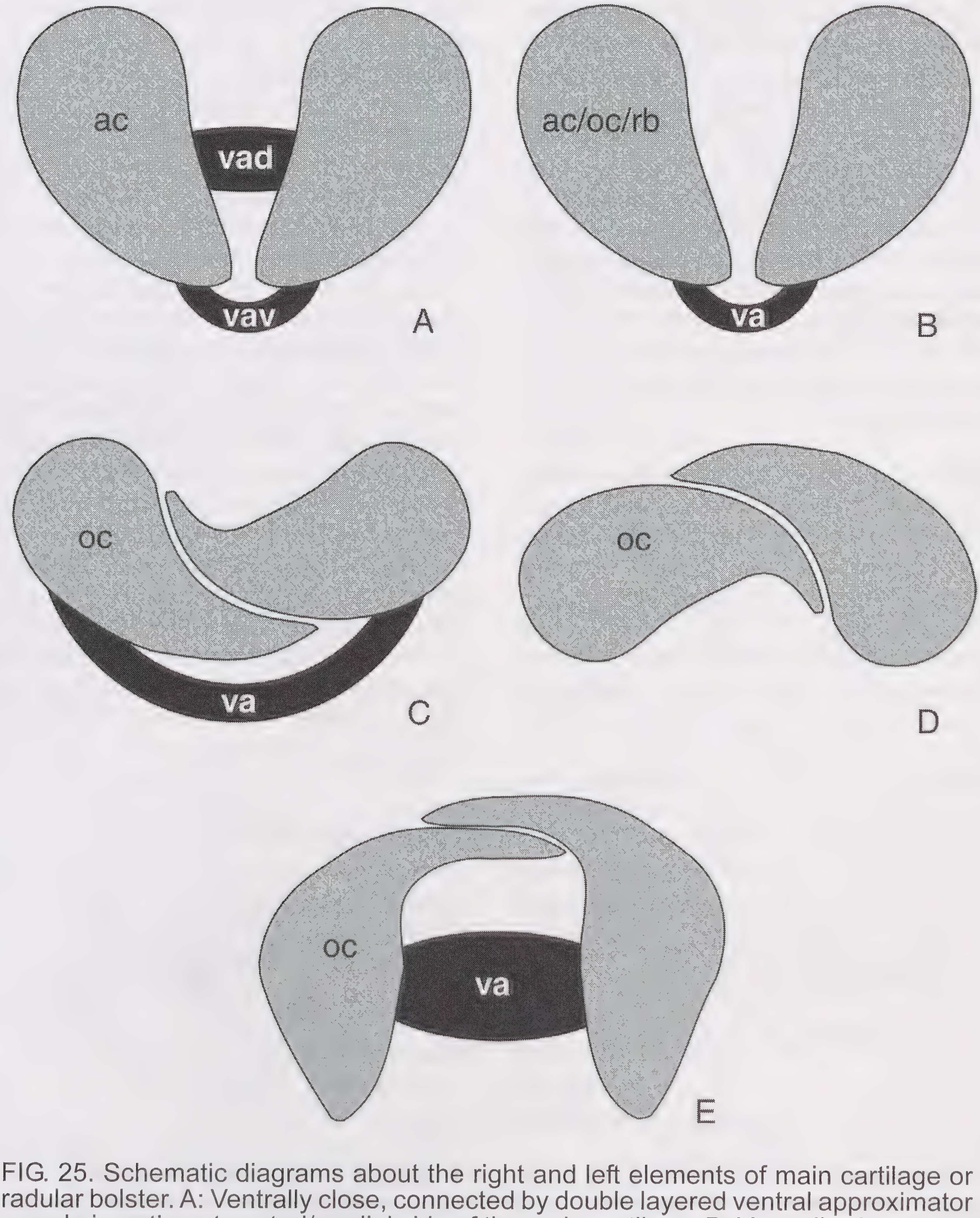

FIG. 25. Schematic diagrams about the right and left elements of main cartilage or radular bolster. A: Ventrally close, connected by double layered ventral approximator muscle inserting at ventral/medial side of the main cartilage; B: Ventrally close, connected by single layered ventral approximator muscle inserting at ventral side of the main cartilage or radular bolster; C: Ventrally close, connected by single layered ventral approximator muscle inserting at outer lateral side of the main cartilage; D: Dorsally close, muscular connection is absent; E: Dorsally close, connected by single layered ventral approximator muscle inserting at medial side of the main cartilage.

classified into two types; overlapping or not. While the former condition is frequently observed in taenioglossate Caenogastropoda (Appendix), the latter is found in other Gastropoda.

(5) *Closest position of the main cartilage or radular bolster in the buccal mass* (see Fig. 25): The main pairs of cartilages or muscular radular bolsters may be closest ventrally or medially, depending on the taxon. Most species observed have ventrally proximal cartilages or radular bolsters. However, dorsally proximal cartilages or radular bolsters with a convex cross-sectional form are found in some taenioglossate caenogastropods such as *Hipponix* (Hipponicidae), *Fusitriton* (Ranellidae), *Glossaulax* (Naticidae) and *Strombus* (Strombidae) (e.g., Figs. 9C, 11A, B, 12). Outgroup comparison suggests that ventrally proximal cartilages are found throughout Mollusca, except some taenioglossate caenogastropods. These two different types in Caenogastropoda might be functionally significant but this meaning cannot be clearly elucidated from the limited data in this study.

(6) *Insertion of Ventral Approximator Muscle*: The insertion area of the ventral approximator muscle on the odontophoral cartilages or radular bolsters is categorized into three types, ventral, median, and outer lateral ones in gastropods (Fig. 25). The insertion area of the ventral approximator muscle is at the ventral level of the anterior pair of cartilages in Cocculiniformia, Vetigastropoda, Neritimorpha, Neogastropoda, Pulmonata and of the ventral layer of *Cellana* (Nacellidae). The ventral approximator muscles in *Fusitriton* (Ranellidae) and the dorsal layer of this muscle in *Cellana* insert at the inner medial wall of the cartilages. The insertion of these muscles at the outer lateral zone is unique to Caenogastropoda except for Neogastropoda.
The state in outgroups (e.g., Wingstrand, 1985) indicates that the insertion of the ventral approximator muscle at the median or ventral side of the cartilage is the plesiomorphic condition for gastropods.

Homology

The homology of different cartilages or radular bolsters has been discussed in terms of topological relationship, histology, and muscle connection (Graham, 1964, 1973; Wingstrand, 1985; Salvini-Plawen, 1988; Sasaki, 1998; Guralnick & Smith, 1999).

Within gastropods, homology can be established between the anterior cartilages of basal gastropods and a single pair or fused cartilage in caenogastropods on the basis of their topological correspondence. For the same reason, the single pair or single fused cartilage of membrane-enclosed radular bolster in Pulmonata can be regarded as a secondarily modified homologous structure of an anterior/odontophoral cartilage. These cartilages similarly support the main part of the odontophore and are connected by the ventral approximator muscle. The cartilages observed in "Aplacophora" (Scheltema et al., 1994) and Scaphopoda (Salvini-Plawen, 1988: 363, fig. 29; Shimek & Steiner, 1997; Fig. 24) seems to be the homologue of the anterior cartilages of basal gastropods based on topology.

The homology of polyplacophoran, monoplacophoran and patellogastropod radular-supporting structures has been interpreted in different ways. According to Graham (1964) and Wingstrand (1985), the anterior cartilage of Patellogastropoda is the homologue of the polyplacophoran and monoplacophoran radular vesicle. However, we question this hypothesis for two reasons, (1) there is no histological evidence to support their interpretation, and (2) in Polyplacophora and Monoplacophora, the ventral approximator muscle inserting at the inner cartilages, not from the radular vesicles (Fig. 24). This latter fact, in particular, supports the homology between the anterior cartilages of patellogastropods and the inner cartilages of polyplacophorans and monoplacophorans.

Graham (1964) argued that the anterior cartilages of *Patella* is derived from the radular vesicle by secondary filling of cartilaginous tissue, on the ground that the cells of anterior cartilage of *Patella* are notably smaller that those of other cartilages. Wingstrand (1985) supported Graham's (1964) hypothesis, and also stated that the anterior cartilage of *Patella* is the homologue of the radular vesicle and medial (= inner) cartilages. A similar histology of cartilages was also found in *Cellana* in this study (Fig. 2D), and Graham's (1964) and Wingstrand's (1985) hypothesis seems to be supported. However, in the species of Acmaeoidea, the histology of the anterior cartilages is the same as those of other cartilages and also other basal gastropods (e.g., Sasaki et al., 2006b). Therefore, Graham's (1964) and Wingstrand's (1985) scenario is applicable only to the Patellidae and Nacellidae and does not apply to patellogastropods as a whole.

The homology of anterolateral cartilages of patellogastropods and outer cartilages of polyplacophorans and monoplacophorans has been suggested by various previous authors (Wingstrand, 1985: 62–66; Salvini-Plawen, 1988: 359–360, Guralnick & Smith, 1999: 184; Table 3). This view is supported by the fact that the anatomical location of the outer cartilages is approximately the same as that of the anterolateral cartilage (Figs. 2A, B, 24A, B). Similarly, polyplacophoran and monoplacophoran inner cartilages seem to be the homologue of anterior cartilages of patellogastropods, because they have similar topology in buccal mass and connected by the ventral approximator muscle.

Systematic Implications

Morphological comparison according to taxonomic grouping (Appendix, Table 2) revealed that most major gastropod groups have characteristic combinations of character states of the odontophoral cartilages or radular bolsters.

Patellogastropoda: The odontophoral cartilages of patellogastropods are mainly characterized by (1) more than one pair of cartilages (two to five pairs), (2) the presence of anterolateral cartilages, and (3) the two layers of the ventral approximator muscle (except *Bathyacmaea*: Sasaki et al., 2006b) inserting on the ventral and medial levels of the anterior cartilages.

Vetigastropoda: The majority of vetigastropods have two pairs of cartilages which consist of anterior and posterior pairs (Haszprunar 1987a, 1988b; Sasaki, 1998; this study). However, exceptions to this generalization are seen in lepetelloideans and "hot-vent" vetigastropods; for example, the anterior and anterodorsal cartilages in *Choristella* (Haszprunar, 1992) and *Bathyphytophilus* (Haszprunar & McLean 1996), a single pair in *Osteopelta* (Haszprunar, 1988c), *Neomphalus* (Fretter et al., 1981) and *Lepetodrilus* (Sasaki, 1998), and two pairs (anterior and anterodorsal) plus single median cartilage in *Cocculinella* (Haszprunar, 1988c). Other characters, such as histology and the closest point of the anterior pairs, are similar to those of patellogastropods and Neritimorpha.

TABLE 3. Statements on patellogastropod cartilages in past studies. (-: no statement).

Reference	Anterior cartilages	Anterolateral cartilages	Posterior cartilages
Graham, 1964: p. 326	= mono-/polyplacophoran radular vesicle (based on histology)	-	-
Windstrand, 1985: pp. 62–66	= mono/polyplacophoran radular vesicle and medial cartilage (based on histology, topology)	= mono/polyplacophoran lateral cartilage (based on topology)	= posterior part of polyplacophoran lateral cartilage (based on insertion of some homologous muscles)
Salvini-Plawen, 1988: pp. 359–360	= mono/polyplacophoran medial cartilage (based on topology)	= mono/polyplacophoran lateral cartilage (based on topology)	-
Guralnick & Smith, 1999: p. 184	plesiomorphic for Mollusca (based on position, shape and composition)	plesiomorphic for Mollusca, = mono-/polyplacophoran lateral cartilage (based on position, shape and composition)	-

Cocculiniformia: This group (in its restricted sense) is characterized by having a single pair of cartilages with type 2 histology (Haszprunar, 1987b; Sasaki, 1998; this study). Other characters are similar to those of other basal gastropods.

Neritimorpha: The odontophoral cartilages of Neritimorpha are unique in having a single median cartilage embedded in the ventral approximator muscle between the anterior and posterior cartilages (Sasaki, 1998; Kano & Kase 2002; Sasaki et al., 2006a). Other characters are not clearly different from other basal gastropods.

Caenogastropoda: "Lower" Caenogastropoda generally have a single pair of odontophoral cartilages (Appendix; Simone, 2001, 2004a, b), but the cartilages are fused at anterior end, separated, or lost in Neogastropoda (Appendix; Taylor et al., 1993: 133; Kantor et al., 1997; Strong, 2003: character 13). The cartilages are missing in part of Conoidea, and this phenomenon is presumably related to the specialized venom-injecting mode of feeding with a harpoon-like radular tooth. In ptenoglossan families, some parasitic Eulimidae also lacks the entire buccal mass due to the reduction of mechanical feeding organ (Sasaki et al., 2007; see also Warén, 1984). Thus, the loss of the cartilages and odontophore can happen in some groups with specialized feeding habit.

Within odotnophore-bearing caenogastropods, two groups can be recognized histologically. (1) In caenogastropods with a taenioglossate radula, the cartilages have type 3 or 4 histology. (2) The members of the clade Neogastropoda have type 5 histology defined by large nuclei in the cartilage cells surrounded by distinct matrix.

The connection of the ventral approximator muscle is always on the ventral side in Neogastropoda, but highly variable from ventral to outer lateral side in taenioglossate groups.

Odontophoral cartilages with distinctive histology (type 4) are found in Cypraeidae in which the cartilage tissue is characterized by the existence of an extracellular matrix substance that fills large spaces between the cartilage matrices. In addition to *Cypraea boivinii* (Fig. 8), we also confirmed that *Cypraea gracilis japonica* has similar histology (personal observation), excluding the possibility of an abnormality or an exceptional species-specific state. It is uncertain whether or not other closely related taxa such as Ovulidae have the same type of histology.

Heterobranchia: As well documented in past studies (Hyman, 1967: 453; Haszprunar, 1985a, b, 1988a; Ponder, 1990a, b, 1991; Salvini-Plawen, 1988: 332; Luchtel et al., 1997; Ponder & Lindberg, 1997: 145), the buccal mass of Heterobranchia lacks true cartilages and is filled with fibrous connective tissue and muscle fibers (Figs. 17–22). As discussed by Mackenstedt & Märkel (2001: 216–217), this type of histology probably allows radular bolsters to change their shape flexibly during feeding due to their muscular nature.

Although our observations on heterobranchs are limited, the taxa examined fall into two groups. In all but one of the Opisthobranchia examined, the radular bolsters are not clearly separated from the surrounding tissue (Figs. 17–18). In contrast, in the pulmonates, the bolsters are clearly demarcated by a membrane (Figs. 19–22). The exception in the opisthobranchs is the nudibranch *Hypselodoris,* the radular bolsters of which are similar in structure to those seen in Pulmonata (Fig. 18E, F). The significance of these two types should be investigated more extensively throughout the heterobranchs in future studies.

The situation in the lower heterobranchs (Heterostropha) is unclear as no non-euthyneuran taxa were investigated in this study. However, published studies indicate that these taxa too lack either a buccal mass or true cartilages (see Appendix for references).

Evolution of Radula-Supporting Organs in Gastropoda

The evolution of radula-supporting organs in Gastropoda can be reconstructed by outgroup comparison and tracing the character states on recently published phylogenetic trees (Ponder & Lindberg, 1997, for gastropods; Sasaki, 1998, for basal gastropods; Dayrat & Tillier, 2002, for Heterobranchia; Strong, 2003 for Caenogastropoda).

A common gastropod ancestor is inferred to possess a combination of the following plesiomorphic states in the odontophore: (1) two pairs of the odontophoral cartilages, (2) unfused right and left elements, (3) type-1 histology (see above), (4) the ventral insertion of the ventral approximator muscle; and (5) clear demarcation of odontophoral cartilages from the surrounding odontophoral musculature.

During the course of evolution in gastropods, the number of odontophoral cartilages has been greatly diversified. The cartilages have increased in part of Patellogastropoda (Patellidae and Nacellidae), part of Vetigastropoda (Cocculinellidae), and Neritimorpha, and in contrast, fused or lost in Neogastropoda, or replaced by muscles and fibrous connective tissue in Heterobranchia. In earlier studies, Hyman (1967: 241) stated that the presence of several radular bolsters (odontophoral cartilages) is primitive, and that the reduction to one pair due to fusion is a derived condition. Meanwhile, Salvini-Plawen (1988: 359–360) advocated that higher numbers of cartilages in Patellidae and one pair or single fused pair in neomphalid or caenogastropod cartilages are secondary products. Similarly, Ponder & Lindberg (1997: 146) also regarded the increase in cartilage number as secondary. In accordance with these recent studies, the latter scenario is better supported in this study.

Evolutionary changes of radula-supporting structures at a histological level have been rarely discussed in the past. In this study, primitive type-1 histology of basal groups is assumed to have been modified into types 3, 4, 5 in Caeogastropoda and type 6 in Heterobranchia, respectively.

The odontophoral cartilages or radular bolsters are enclosed by a sheath of collagen fibers in all gastropods other than some opisthobranchs (Haminoeidae, Philinidae, Cylichnidae, Cavoliniidae, and Aplysiidae: Figs. 17, 18A–D; Appendix). Thus, ensheathed cartilages are regarded as original gastropod condition, and the loss of the sheath is apomorphic change occurred in part of Opisthobranchia.

The differences in the insertion areas of the ventral approximator muscle seem to be related to the lateral rotation of the main cartilages during feeding. Ventrolateral insertion allows lateral rotation of the radula (Fretter & Graham, 1962; Hyman, 1967; Graham, 1973; Salvini-Plawen, 1988), but doso- or ventromedial insertion does not. The former insertion is regarded as advanced and observed frequently in Gastropoda, except for taenioglossate caenogastropods, which have outer lateral insertion. The insertion of the ventral approximator muscle might be one factor affecting the mode of feeding as Salvini-Plawen (1988) stated, but at present we are unable to give a detailed account.

A correlation between morphological types of the radula-supporting organs and modes of feeding is clearly rejected in most cases. For example, various herbivorous gastropods belonging to Patellogastropoda, Vetigastropoda, *Aplysia* and *Siphonaria* have distinctive morphology and/or histology that is specific to each higher taxonomic category. Similarly, species in the caenogastropod Littorinimorpha share similar cartilage morphology and histology but show highly diverse modes of feeding such as grazing in *Littorina*, shell boring in Naticidae, deposit feeding in Strombidae, ciliary feeding in Calyptraeidae and carnivory in Ranellidae. Thus, there is no direct connection between odontophoral cartilage morphology/histology and feeding ecology in gastropods.

Major habitat selection is also unrelated to morphological diversification of radular supporting organs. Different freshwater or terrestrial groups do not fall into the same category but share similar structures with phylogenetically closer members in marine environments. Accordingly, the morphological diversity in radula-supporting organs must be a phylogenetically constrained phenomenon.

In conclusion, the diversification of gastropod radula-supporting structures is virtually controlled by phylogeny regardless of feeding ecology and habitat. The functional differentiation of the odontophore must be considered in connection with comparative anatomy of buccal musculature and development of different types of proboscis in future studies.

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APPENDIX

Character states of cartilages or radular bolsters in gastropods and other molluscs. ac: anterior cartilage, vc: ventral cartilage, alc: anterior lateral cartilage, pc: posterior cartilage, pdc: posterodorsal cartilage, mc: median cartilage, adc: anterodorsal cartilage, ic: inner cartilage, oc: outer cartilage, ?: uncertain, -: cartilages absent. *Warén & Bouchet (2001).

Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Aplacophora								
Simrothiellidae	*Helicoradomenia juani*	2	muscle and collagen fibers with cartilage-like cells	present	absent	ventral?	unclear	Scheltema et al. (1994)
Limifossoridae	*Scutopus robustus*	2	muscle and collagen fibers	?	absent	?	?	Scheltema et al. (1994)
Polyoplacophora								
Ischnochitonidae	*Schizoplax* sp.	4 (ic, ouc)	?	present	absent	ventral?	ventral/inner median	Wingstrand (1985)
Ischnochitonidae	*Ischnochiton comptus*	4 (ic, ouc)	thin matrix and cartilage cells	present	absent	ventral	inner median	This study (Figs. 24A–B)
Leptochitonidae	*Lepidopleurus asellus*	4 (ic, ouc)	thin matrix and cartilage cells	present	absent	ventral?	ventral/inner median	Wingstrand (1985)
Monoplacophroa								
Vemidae	*Vema ewingi*	4 (ic, ouc)	?	present	absent	ventral?	ventral/ inner median	Wingstrand (1985)
Neopilinidae	*Neopilina galatheae*	4 (ic, ouc)	?	present	absent	ventral?	ventral/inner median	Wingstrand (1985)
Neopilinidae	*Laevipilina antarctica*	2	?	present	absent	median	?	Schaefer & Haszprunar (1996: figs. 2, 9)
Micropilinidae	*Micropilina arntzi*	2	thin matrix and cartilage cells	present	absent	?	?	Haszprunar & Schaefer (1996: figs. 2–4, 9)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Scaphopoda								
Rhabdidae	*Rhabdus rectius*	2	?	present	absent	ventral	ventral	Shimek & Steiner (1997)
Gadilidae	*Gadila aberrans*	2	large fluid-filled cells?	present	absent	ventral	ventral	Shimek & Steiner (1997)
Dentaliidae	*Dentalium octanglatum*	2	fibrous connective tissue and musclar fibers	present	absent	dorsal	dorsal	This study (Fig. 24C–D)
Gadilinidae	*Episiphon subrectum*	2	fibrous connective tissue and musclar fibers	absent	absent	ventral	ventral	This study (Figs. 24E–F)
Patellogastropoda								
Patellidae	*Scutellastra flexuosa*	6 (ac, alc, pc)	?	present	absent	ventral	inner median?	Sasaki (1998: figs. 2a–c)
Patellidae	*Patella vulgata*	10 (ac, vc, alc, pc, pdc)	?	present	absent	?	inner median/ ventral	Graham (1964: figs. 5, 7–11, 13)
Nacellidae	*Cellana grata*	10 (ac, vc, alc, pc, pdc)	type 1	present	absent	ventral	inner median/ ventral	This study (Figs. 1A, 2)
Nacellidae	*Cellana toreuma*	10 (ac, vc, alc, pc, pdc)	?	present	absent	?	?	Sasaki (1998: fig. 7a)
Lepetidae	*Limalepeta lima*	4 (ac, alc)	?	present	absent	ventral	inner median/ ventral	Sasaki (1998: fig. 14b)
Acmaeidae	*Pectinodonta orientalis*	4 (ac, alc)	?	present	absent	ventral	inner median/ ventral	Sasaki (1998: figs. 17a–b)
Acmaeidae	*Bathyacmaea secunda*	4 (ac, alc)	type 1	present	absent	ventral	ventral	Sasaki et al. (2006b: figs. 8B–C)
Acmaeidae	*Niveotectura pallida*	4 (ac, alc)	?	present	?	ventral	inner median?	Sasaki (1998: fig. 18c)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Vetigastropoda								
Fissurellidae	*Scutus sinensis*	4 (ac, pc)	?	present	absent	ventral	ventral	Sasaki (1998: figs. 36a–b)
Haliotidae	*Haliotis diversicolor aquatilis*	4 (ac, pc)	type 1	present	absent	ventral	ventral	This study (Figs. 1B, 3)
Haliotidae	*Sulculus diversicolor aquatilis*	4 (ac, pc)	?	present	absent	ventral	ventral	Sasaki (1998: figs. 31c–d)
Bathyphytophilidae	*Bathyphytophilus diegensis*	4 (ac, adc)	type 2 (ac), ? (adc)	present	absent?	ventral	?	Haszprunar & McLean (1996: figs. 16–17)
Choristellidae	*Choristella hickmanae*	4 (ac, adc)	type 3?	present	absent	?	?	Haszprunar (1992: figs. 3, 5)
Cocculinellidae	*Cocculinella minutissima*	5 (ac, adc, single mc)	type 2 (ac), ? (adc), ? (mc)	present	absent?	ventral	ventral	Haszprunar (1988c: figs. 5, 7, 11, 13)
Osteopeltidae	*Osteopelta mirabilis*	2	?	present	absent	?	?	Haszprunar (1988c: fig. 16)
Lepetellidae	*Addisonia lateralis*	4 (ac, pc)	?	present	?	?	?	Haszprunar (1987a: fig. 4A)
Pseudococculinidae	*Kurilabyssia venezuelensis*	4 (ac, pc)	?	present	absent	?	ventral	Haszprunar (1988b: fig. 3)
Pseudococculinidae	*Amphiplica knudseni*	4 (ac, pc)	?	present	?	?	?	Haszprunar (1988b: fig. 4)
Lepetodrilidae	*Lepetodrilus nux*	2	?	present	absent	ventral	ventral	Sasaki (1998: figs. 63c–d)
Lepetodrilidae	*Lepetodrilus pustulosus*	at least 2 pairs	?	present	?	?	?	Fretter (1988)
Lepetodrilidae*	*Clypeosectus delectus*	4 (ac, pc)	type 1	present	absent	ventral	ventral?	Haszprunar (1989b: fig. 4A)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Lepetodrilidae*	*Pseudorimula marianae*	4 (ac, pc)	type 1	present	absent	ventral	ventral?	Haszprunar (1989b: figs. 8A, C, 9A)
Lepetodrilidae*	*Gorgoleptis emarginatius*	at least 2 pairs	?	present	?	?	?	Fretter (1988: fig. 17)
Sutilizonidae	*Temnocinclis euripes*	4 (ac, pc)	type 1	present	absent	ventral	ventral?	Haszprunar (1989b: figs. 1A–B)
Neomphalidae	*Neomphalus fretterae*	2	?	present	absent?	?	?	Fretter et al. (1981: figs. 4–5)
Peltospiridae	*Rhynchopelta concentrica*	2	?	present?	absent	ventral	ventral	Fretter (1989: figs. 4–5)
Peltospiridae	*Melanodrymia aurantiaca*	at least 1 pair	type 3?	present	?	?	?	Haszprunar (1989a: figs. 2, 4–5, 8)
Pleurotomariidae	*Midotrochus beyrichii*	4 (ac, pc)	?	present	absent	ventral	ventral	Sasaki (1998: fig. 25d)
Trochidae	*Monodonta labio confusa*	4 (ac, pc)	type 1	present	absent	ventral	ventral	This study (Fig. 4)
Trochidae	*Chlorostroma lischkei*	4 (ac, pc)	?	present	absent	ventral	ventral	Sasaki (1998: figs. 53a–b)
Cocculiniformia								
Cocculinidae	*Cocculina* sp. cf. *japonica*	2	type 2	present	absent	ventral	ventral	This study (Figs. 5A–B)
Cocculinidae	*Cocculina nipponica*	2	?	present	absent	ventral	ventral	Sasaki (1998: fig. 69d)
Cocculinidae	*Coccopygya hispida*	2	?	present	absent	ventral	ventral	Haszprunar (1987b: fig. 3)
Neritimorpha								
Neritidae	*Nerita albicilla*	5 (ac, pc, mc)	type 1 (ac, pc), type 3 (mc)	present	absent	ventral	ventral	Sasaki (1998: figs. 75c–d), this study (Figs. 1C, 5C–D)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Neritiliidae	*Pisulina adamsiana*	5 (ac, pc, mc)	?	?	absent	?	ventral	Kano & Kase (2002: fig. 5E)
Helicinidae	*Waldemaria japonica*	5 (ac, pc, mc)	?	present	absent	ventral	ventral	Sasaki (1998: figs. 89c–d)
Phenacolepadidae	*Cinnalepeta pulchella*	5 (ac, pc, mc)	?	present	absent	ventral	ventral	Sasaki (1998: figs. 83a–b)
Phenacolepadidae	*Shinkailepas myojinensis*	5 (ac, pc, mc)	type 1	present	absent	ventral	ventral	Sasaki et al. (2006a: figs. 8A–B)
Taenioglossate Caenogastropoda								
Provannidae	*Provanna variabilis*	2	type 3	present	?	?	?	Warén & Ponder (1991: figs. 9A, 10A, 11C)
Cyclophoridae	*Cyclophorus herklotsi*	2	type 3	present	present	ventral	outer lateral	This study (Figs. 6A–B)
Viviparidae	*Cipangopaludina chinensis laeta*	2	type 3	present	present	ventral	outer lateral	This study (Figs. 1D, 6C–D)
Ampullariidae	*Marisa cornuarietis*	2	type 3	present	?	ventral	?	Berthold (1991: figs. 250, 287)
Ampullariidae	*Afropomus balanoudeus*	2	?	present	present	?	outer lateral	Berthold (1991: figs. 247, 249)
Ampullariidae	*Saulea vitrea*	2	?	present	?	?	?	Berthold (1991: fig. 248)
Batillariidae	*Batillaria cumingii*	2	type 3	present	present	ventral	outer lateral	This study (Figs. 7A–B)
Calyptraeidae	*Crepidula onyx*	2	type 3	present	absent	ventral	outer lateral	This study (Figs. 1F, 7C–D)
Cypraeidae	*Cypraea boivinii*	2	type 4	present	absent	ventral	ventral	This study (Figs. 1G, 8)
Littorinidae	*Littorina brevicula*	2	type 3	present	present	ventral	outer lateral	This study (Figs. 1E, 9A–B)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Naticidae	*Glossaulax didyma*	2	type 3	present	present	dorsal	absent	This study (Figs. 9C–D)
Assimineidae	*Assiminea japonica*	2	type 3	present	absent	ventral	?	This study (Figs. 10A–B)
Hydrobiidae	*Pomatiopsis lapidaria*	2	?	?	?	?	?	Davis (1967: pl. 17, figs. 3, 5)
Hydrobiidae	*Onchomelania hupensis*	2	?	?	?	?	?	Davis (1967: pl. 28, fig. 4)
Strombidae	*Strombus luhuanus*	2	type 3	present	present	dorsal	absent?	This study (Figs. 10C–D)
Ranellidae	*Fusitriton oregonensis*	2	type 3	present	present	ventral	inner median	This study (Fig. 11)
Hipponicidae	*Hipponix conica*	2	type 3	present	present	dorsal	absent	This study (Figs. 12A–B)
Vermetidae	*Serpulorbis imbricatus*	2	type 3	present	present	ventral	outer lateral	This study (Figs. 12C–D)
Ptenglossa								
Janthinidae	*Janthina janthina*	2	?	?	absent	ventral	ventral?	Graham (1965: figs. 2, 8–9)
Eulimidae	*Asterophila japonica*	0	-	-	-	-	-	Sasaki et al. (2007)
Neogastropoda								
Buccinidae	*Japeuthria ferrea*	1 (fused)	type 5	present	absent	ventral	ventral	This study (Fig. 13)
Columbellidae	*Euplica scripta*	1 (fused)	type 5	present	absent	ventral	ventral	This study (Fig. 14)
Columbellidae	*Mitrella burchardi*	2	?	?	?	?	?	Kantor & Medinskaya (1991: fig. 2A)
Nassariidae	*Nassarius festiva*	1 (fused)	type 5	present	absent	ventral	ventral	This study (Fig. 15)
Muricidae	*Thais clavigera*	1 (fused)	type 5	present	absent	ventral	ventral	This study (Figs. 1H, 16A–D)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Marginellidae	*Mesoginella pygmaea*	1 (fused)	?	?	?	?	?	Ponder (1970: fig. 2B)
Marginellidae	*Volvarina mustelina*	1 (fused)	?	?	?	?	?	Ponder (1970: fig. 2I)
Mitridae	*Strigatella zebra*	2	type 5	present	absent	ventral	ventral	This study (Figs. 1L, 16E–F)
Mitridae	*Strigatella paupercula*	2	?	present?	absent?	ventral	?	Ponder (1972: fig. 1B)
Volutomitridae	*Peculator dedleyi*	2	?	?	?	?	?	Ponder (1972: fig. 7A)
Volutomitridae	*Volutomitra alaskana*	2	?	?	?	?	?	Kantor & Harasewych (1992: fig. 5)
Olivellidae	*Olivella borealis*	2	?	?	?	?	?	Kantor (1991: fig. 5C)
Pseudolividae	*Pseudoliva ancilla*	2	?	?	?	?	?	Kantor (1991: fig. 13A)
Strictispiridae	*Strictispira paxillus*	2	type 5	?	?	?	?	Kantor & Taylor (1994: figs. 1, 2A)
Terebridae	*Hastula bacillus*	1 (fused)	?	?	?	?	?	Taylor & Miller (1990: fig. 7)
Conidae	*Conus ebraeus*	0	-	-	-	-	-	This study
Heterobranchia								
Orbitestellidae	*Microdiscula ccharopa*	0	?	?	?	?	?	Ponder (1990a)
Architectonicidae	*Heliacus variegatus*	0	?	?	?	?	?	Haszprunar (1985a)
Glacidorbidae	*Glacidorbis hedleyi*	0	?	?	?	?	?	Ponder (1986)
Mathildidae	*Opimilda maoria*	0	?	?	?	?	?	Haszprunar (1985b)

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Higher Taxa	Species	Number of cartilages or radular bolsters	Histology	Membrane enclosing cartilage or radular bolster	Overlapping of right and left main cartilages or radular bolsters	Closest position of main cartilages or radular bolsters	Insertion of ventral approximator muscle	Reference
Amathinidae	*Amathina triccarinata*	0	?	?	?	?	?	Ponder (1987)
Cornirostridae	*Cornirostra pellucida*	0	?	?	?	?	?	Ponder (1990b)
Haminoeidae	*Haloa japonica*	0	type 6	absent	absent	-	absent	This study (Figs. 17A–B)
Philinidae	*Philine argentata*	0	type 6	absent	absent	-	absent	This study (Figs. 17C–D)
Cylichnidae	*Nipponoscaphander japonica*	0	type 6	absent	absent	-	absent	This study (Figs. 17E–F)
Cavoliniidae	*Cavolinia uncinata*	0	type 6	absent	absent	-	absent	This study (Figs. 18A–B)
Aplysiidae	*Aplysia oculifera*	0	type 6	absent	absent	-	absent	This study (Figs. 18C–D)
Chromodorididae	*Hypselodoris festiva*	2	type 6	present	absent	ventral	absent	This study (Figs. 18E–F)
Siphonariidae	*Siphonaria japonica*	1 (fused)	type 6	present	absent	ventral	ventral	This study (Fig. 19)
Siphonariidae	*Williamia gussonii*	2	type 6	present	absent	ventral	ventral	Ruthensteiner (2006: fig. 2A)
Lymnaeidae	*Lymnaea stagnalis*	1 (fused)	type 6	present	absent	ventral	ventral	This study (Fig. 20)
Onchidiidae	*Peronia* sp. cf. *verruculatum*	2	type 6	present	absent	ventral	ventral	This study (Figs. 1J, 21)
Bradybaenidae	*Acusta despecta sieboldiana*	1 (fused)	type 6	present	absent	ventral	ventral	This study (Figs. 1K, 22)